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VARIATION AND HYBRIDIZATION IN SOUTHERN CALIFORNIA POPULATIONS OF DIPLACUS (SCROPHULARIACEAE)[1]

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INTRODUCTION

Diplacus, an attractive spring-flowering soft-wood perennial in the family Scrophulariaceae, is a common semi-shrub in the summer-dry vegetation of the Pacific Coast. Due to its shrubby habit, close relationship to, and periodic inclusion in the genus *Mimulus, Diplacus* has acquired the common name of Woody or Shrub Monkey-flower. The genus has a north-south distribution range of over 1,250 miles, varying from the cool, humid coast of southern Oregon to the dry, warm climate of northern Baja California. *Diplacus* occurs from sea level along the coast to over 7,000 feet on some of the inland mountains (fig. 1). In California, the center of its geographical range, it is distributed widely on five of the eight Channel Islands; throughout most of the hills, foothills, and mountains along the entire coast; and inland, a maximum of 150 miles, to the cismontane slopes of the Sierra Nevada and the westernmost margins of the Mojave and Colorado deserts.

The amount of ecological variation comprised in a Pacific Coast distribution of this kind is indicated by the number of plant communities in which *Diplacus* occurs. Of the 29 California communities described by Munz and Keck (in Munz, 1959), *Diplacus* is found in at least 12. *Diplacus* species also occur in various levels of succession that follow community disturbance. The number of different micro-environments caused by natural and artificial disturbances also adds to the wide ecological spectrum of this group. As could be expected in a variable genus that exists in a wide range of habitats, the size and the density of *Diplacus* populations varies from thousands of individuals dominating entire hillsides, to small restricted populations scattered discontinuously along rocky ridges, cliffs, mountain tops, eroded boulders and outcrops. Even minor ecological differences, either natural or artificial, apparently are of vital importance in the population dynamics of *Diplacus.*

Since the publication of the first species by William Curtis in 1796, the taxonomy of *Diplacus* has been in a perpetual state of flux. Commencing with the generic description (Nuttall, 1838), at least 21 authors have described more than 60 specific or subspecific taxa, 12 incidences under the generic banner of *Dipacus,* and 18 in a section *Diplacus* of the genus *Mimulus.* In the last 26 years, three authors retained the species in *Mimulus* (Adele Grant, 1924; Munz, 1935, 1959; Pennell, 1949, 1951), and two supported their generic separation (Jepson, 1925; McMinn, 1939, 1951). In this study, as the title indicates, *Diplacus* is segregated from the genus *Mimulus* and retained as a genus.

There has been a long history of vacillating species lines in *Diplacus.* Of the above

[1]Based on a thesis presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Claremont Graduate School. The work was done under the supervision of Professor Verne Grant at the Rancho Santa Ana Botanic Garden.

studies, Adele Grant (1924) recognized 8 species and 3 varieties; Jepson (1925), 6 species and 2 varieties; Pennell (1951), 8 species and 2 varieties; McMinn (1951), 13 species; Munz (1959), 7 species, 4 subspecies and 1 variety.[2] Because the morphological range of the genus has not been increased since the addition of *D. calycinus* (Eastwood, 1904), the above changes in species boundaries and nomenclature have resulted principally from varying interpretations of morphological and distributional data.

These taxanomic treatments have been based primarily upon revisions of the studies of Adele Grant (1924) and McMinn (1951). Mrs. Grant treated the entire genus *Mimulus,* including Diplacus, by morphological methods. Howard McMinn, restricting his problem to *Diplacus,* augmented this with an experimental breeding program and a more intensive field survey throughtout its range. To some extent, each realized that hybridization was occurring among some of the wild populations.

As a preliminary to the present study, I attempted to identify the species found in the cismontane foothills of the San Gabriel Mountains north of Claremont and the San Jose Hills south of Glendora by using the available keys and descriptions. The results were often unsatisfactory. In many locations, profuse and unexplained variation was rampant; yet other populations proved to be quite homogeneous. Gradients in flower color and plant habit obviously were correlated with changes in elevations; however, two populations of *Diplacus* 25 miles apart, growing at nearly equal elevations, in similar climates, and with similar plant associations, were characterized by very different modes of plant form and flower color. In a number of variable populations, it was possible, using McMinn's treatment, to identify five "species" of *Diplacus* growing side by side. Varying either the study or the location did little to improve the anomaly. Thus, all previous taxonomic treatments were shelved temporarily while an attempt was made to obtain a workable method for analyzing the morphological variation within and between the populations.

From information derived in the course of this study, I was able to recognize five taxa of *Diplacus* on the mainland of southern California, each sufficiently distinct ecologically and morphologically to be modally identifiable. Although in some cases races with a similar degree of differentiation have been considered ecotypic subspecies (Clausen, Keck, and Hiesey, 1940, for *Potentilla glandulosa*), I shall for the present refer to the ecological modes in *Diplacus* as species (fig. 5–6). Two of them, *Diplacus aridus* and *D. clevelandii,* are localized endemics which are more distinct and perhaps less controversial than the other three: *D. calycinus, D. longiflorus,* and *D. puniceus* (fig. 2–4).

This study mostly concerns the latter three species and is not intended to be a taxonomic revision. It is rather an attempt to supplement previous taxonomic work by acquiring an understanding of the nature and causes of *Diplacus* variation in the southern California populations.

THE GEOGRAPHICAL AREA STUDIED

The investigation was initiated in a complex of *Diplacus* populations existing along the central coast-facing slopes of the San Gabriel Mountains, Los Angeles County, southern California. The geographical limits were later extended until a sufficient number of populations were observed and analyzed to afford a reasonable solution to the problem. The coordinated emphasis upon the individual, the population, and the habitat, however, neces-

[2]For a more complete taxonomic history see Adele Grant (1924) and McMinn (1951).

Fig. 1.—Topographical map of California, southern Oregon, and northern Baja California.—*Upper right:* Mainland distribution of *Diplacus.*—*Lower left:* Insular distribution of *Diplacus* on an expanded scale of the Channel Islands.

FIGURE 1

sitated limiting the number of populations and the size of the geographical area.

Eventually, these limits included many of the cismontane and some of the desert slopes of the San Gabriel, San Bernardino, and Little San Bernardino Mountains of the Transverse Geomorphic Province; and the Santa Ana, San Jacinto, Cuyamaca, and Laguna Mountains of the Peninsular Geomorphic Province.[3] Also incorporated were the Puente and San Jose Hills, which bridge the Santa Ana and San Gabriel Mountains, and the coastal San Joaquin Hills that lie adjacent to, and southwest of the Santa Ana Range (fig. 5).

Within this geographical area, two principal population series were analyzed: (1) The Laguna Series, (2) The San Diego Series. Of them, the Laguna Series occupied the larger area, in which more populations were investigated extensively. Included in this series were the populations of the San Joaquin Hills, the Santa Ana Mountains, Palomar Mountain, the Puente and San Jose Hills, the San Gabriel Mountains, the Little San Bernardino Mountains, and the San Jacinto Mountains. The San Diego Series contained fewer populations over a smaller area. This series progressed inland from Point Loma through the Descanso and Potrero regions, including the southern Cuyamaca and Laguna Mountains, to El Campo and Jacumba. Within this series, the Point Loma, La Mesa, and Lakeside populations were analyzed fully. All measured populations, their locations, and their habitats are listed in table 4.

ECOLOGY

It has been estimated that the amount of ecological variation which exists between the Atlantic Coast and the eastern base of the Rocky Mountains is much less than that which occurs between the base and the summit on one small California mountain. To the uninitiated, this may seem exaggerated, but to the botanist who has struggled with a California introgressant series in its multiplicity of habitats, the statement appears conservative. In the Laguna and San Diego Series, the ecological variation ranges from maritime habitats on the coast, through the chaparral belts of the interior mountains, up to the high elevations in these mountains, and into the deserts beyond.

Though the following is admittedly an oversimplification, I shall classify the habitats of the *Diplacus* populations of southern California into three types:

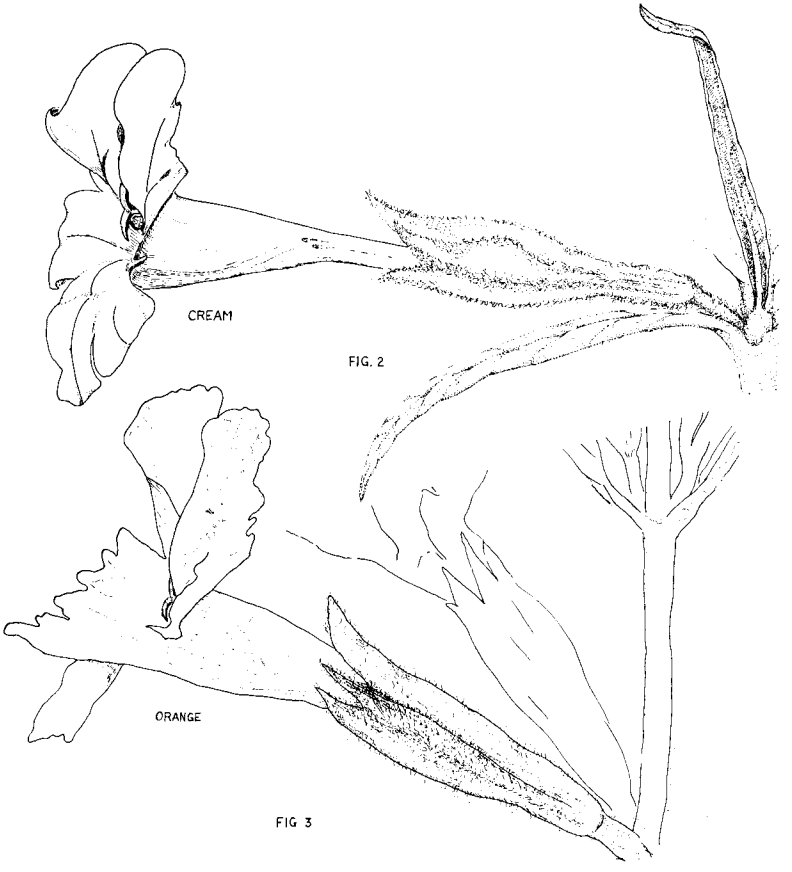
(1) The Temperate Hillside
(2) The Insolated Hillside
(3) The Rock Crevice

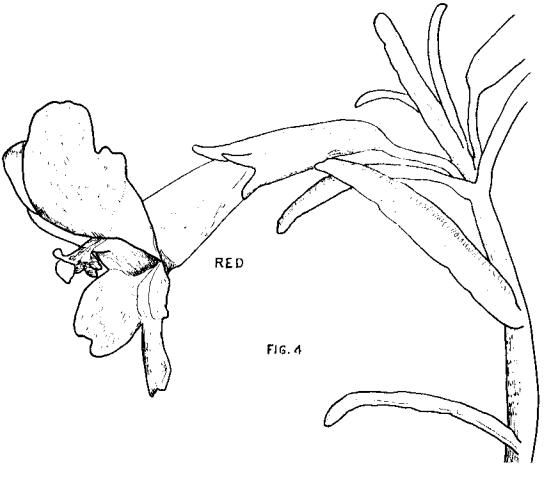
TEMPERATE HILLSIDE HABITAT

Diplacus puniceus (fig. 2) occurs on the slopes of rolling hills, some foothills, eroded fans and mesas of alluvia, and uplifted sedimentaries along the coastal plains from five miles north of Laguna well into Baja California. The most common biotic association appears to be the Coastal Sage Scrub community; however, *D. puniceus* also occurs in low Chaparral and Chaparral-Coastal Sage ecotones. Since the Coastal Sage Scrub usually is riddled with disturbance by rabbits, numerous rodents, and by man, it is difficult to find an area of this community which is not in one or the other stage of succession. It may be, in fact, a community in an early stage of succession adapted opportunistically to such disturbances. *Diplacus puniceus* not only thrives in, but appears to prefer, disturbed niches and

[3]Geomorphological references: Hinds, 1952; Emery, 1954; Jahns, 1954; Miller, 1957.

Fig. 2–4.—Fig. 2. *D. calycinus,* Toll Camp, San Bernardino Mountains.—Fig. 3. *D. longiflorus,* Thompson-Sage, San Gabriel Mountains.—Fig. 4. *D. puniceus,* La Mesa, San Diego County.





FIGURES 2-4

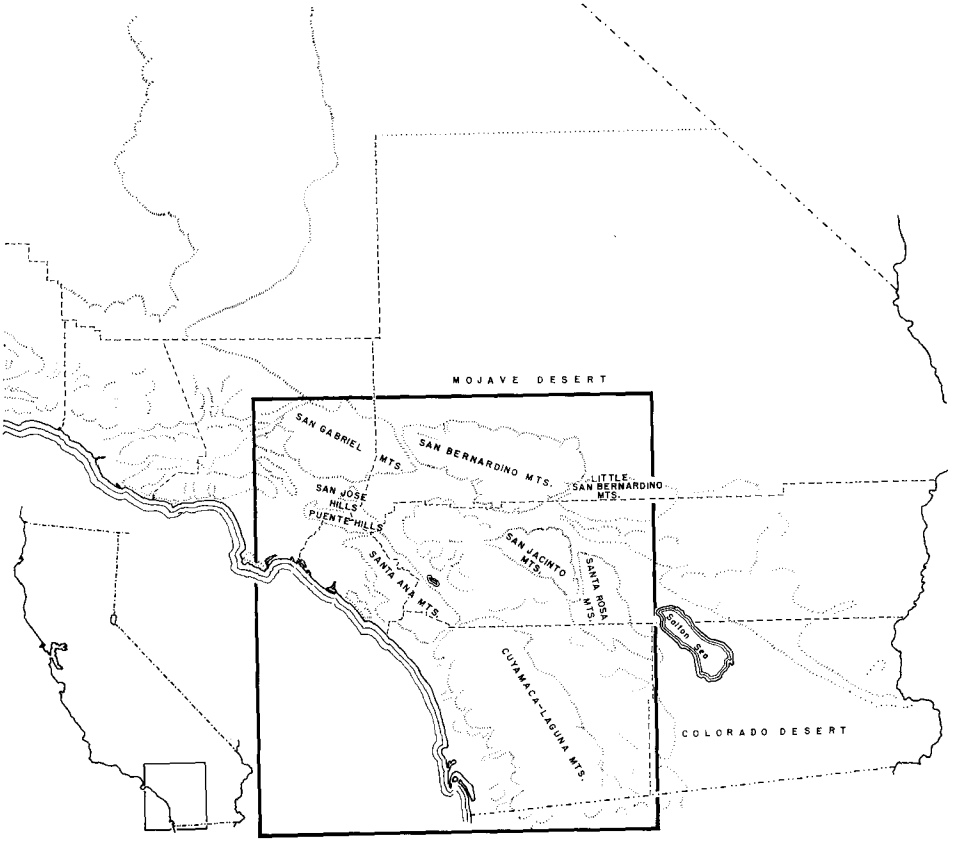


Fig. 5.—Topographic map of Southern California with inset indicating the emphasized area of study.

successfully establishes variable segregants in them. There are, however, two kinds of disturbance in which *D. puniceus* fails to pioneer the secondary succession: (1) fire—when burned to the ground, this species seldom crown sprouts; (2) overgrazing—few if any plants survive extensive cropping and breakage.

The year-round climate of the immediate coastal plains and hills of southern California is moderate and mostly frost-free. The climatic variations of the coast do not exhibit the extremes of the inland regions. The factor basically responsible for this climatic moderation is the prevailing westerly wind from the Pacific Ocean. Besides the atmospheric cooling effect these breezes provide, the fog, as well as lesser amounts of atmospheric humidity, filters and reduces the amount of insolation that is received by the vegetation and the soils. Though the average annual rainfall is only slightly above a desert-producing threshold, the timely spring and early summer fogs provide sufficient protection from evaporation to allow the plants of the region to grow and reproduce. The climatic data for the Coastal Sage Scrub are compared, in table 1, with those of other dominant *Diplacus*-inhabiting communities of southern California.

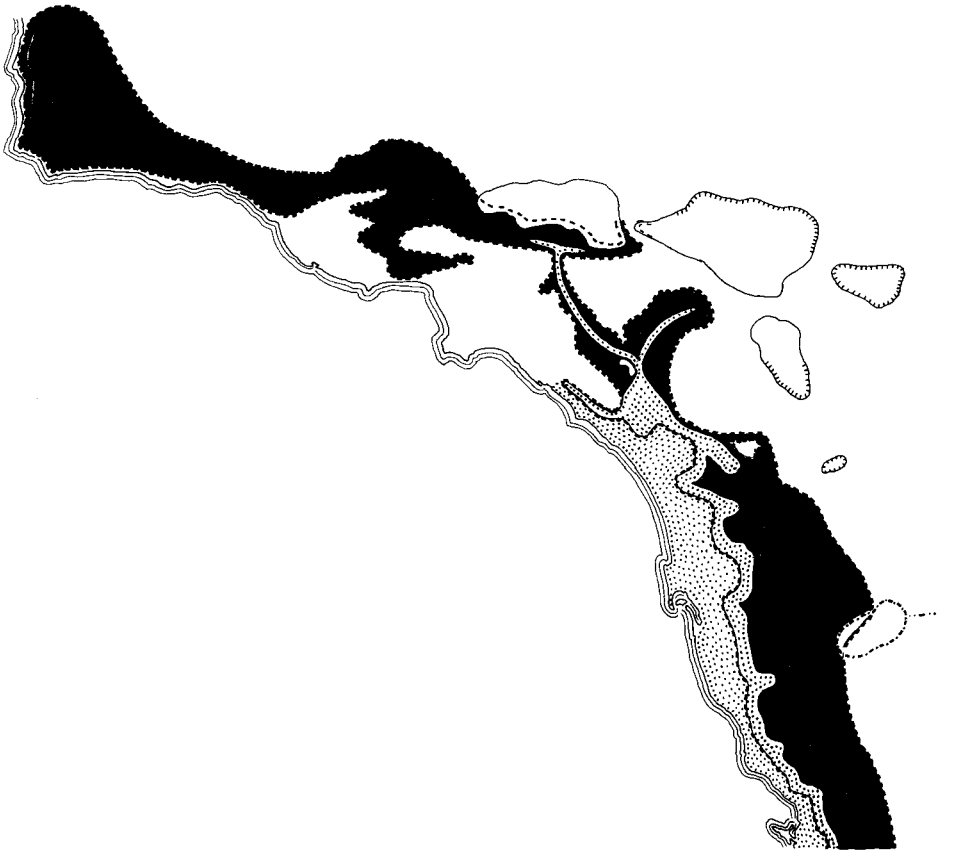


Fig. 6.—Southern California distribution of five *Diplacus* species; *D. puniceus,* stippled; *D. longiflorus,* black; *D. calycinus,* white bound by solid line; *D. aridus,* crosshatch; *D. clevelandii,* distribution in southern part of Cuyamaca and Laguna Mountains and central Santa Ana Mountains is too limited to map. Intergrading between species: *D. puniceus* ⇌ *D. longiflorus,* stippled area behind connected-dash line; *D. longiflorus* ⇌ *D. calycinus,* broken line; *D. calycinus* ⇌ *D. aridus,* perpindicular short line. The two small white areas in Cuyamaca-Laguna Mountains and Santa Ana Mountains are isolated islands of *D. calycinus.*

INSOLATED HILLSIDE HABITAT

The physiographic, edaphic, and biotic factors of this habitat deviate only slightly from those of the Temperate Hillside. Most populations of *D. longiflorus* (fig. 3) continue to compete in communities of Coastal Sage Scrub, low and open Chaparral, ecotones of Chaparral and Coastal Sage Scrub, and expand variably in the open niches of the disturbed habitats. Disturbance and the various stages of succession still are common, deer trails are more numerous, and packrat nests are abundant in the Chaparral; yet, in some locations the vegetation is comparatively more stable. The soils are similar; however, sedimentaries often are missing, and the alluvion of past erosion often is mixed with the residual subsoils of decomposed, metamorphic and igneous parent rock. Occasionally, outcrops of parent rock

become open habitats for numerous *Diplacus* variants. It is here and in other locations of exposed parent rock that the Insolated Hillside habitat begins to merge with the Rock Crevice.

The climate of this environment is more extreme than that of the Temperate Hillside. Less atmospheric humidity, irregularly occurring fogs, and foothill slopes that slant at right angles to the rays of the vernal sun cause substantial increases in the amount of insolation during late spring reproduction. The nightly fall of the dense cold air down the mountain slopes, and the escape of surface heat through the clearer atmosphere result in lower temperatures during the winter. Also, there is a general increase of precipitation which is influenced by the distance from the coast and the steepness of the mountain slope. The climate, as exemplified by the Chaparral and Southern Oak Woodland communities, has the features listed in table 1.

ROCK CREVICE HABITAT

In this niche, *Diplacus calycinus* (fig. 4) becomes a pioneer in primary succession by inhabiting rock crevices. This biologically open habitat is situated in the comparatively more extreme climates of the Desert Woodland and Coniferous Forest. The communities and climates vary considerably within these vegetation types; yet, the selected niche of the mountain and desert *Diplacus* is consistently within the fissures of chrystalline metamorphic or igneous rock. Distribution is controlled mostly by climate; slow succession is the rule. By means of its crown-sprouting behavior, *D. calycinus* can survive ice, wind, heat, and fire. Though the populations tend to be discontinuous, the increase in road-cuts has served to bridge many isolated groups and, in general, to expand the habitat of this taxon. Competition in the surrounding communities affects *D. calycinus* only if the rock is completely decomposed. In table 1, the climates of three local communities, the Yellow Pine Forest, Pinyon-Juniper Woodland, and Joshua Tree Woodland, are compared. *Diplacus* is absent in the lower limits, below 3,000 feet, of the Joshua Tree Woodland.

These three *Diplacus* habitats inevitably overlap. Fingers of the Temperate Hillside creep up the protected sides of inland valleys. Highly insolated southwest-facing foothills of the mountains, though near the coast, provide Insolated Hillside habitats. In the lower foothills, the protected north exposures of road-cuts, and steep stream banks in damp alluvia, or parent rock, provide marginal niches with climates similar to the Rock Crevice Habitat. Occasionally, less steep outcrops of the lower foothills become open niches for segregants from all three habitats. A discussion of the implied taxonomic and evolutionary importance of these habitats and their populations of *Diplacus* will follow.

REPRODUCTION

Diplacus is a genus of interfertile, self-compatible species, the individuals of which are commonly outcrossed, more rarely selfed, by several types of animals. Early records of artificial interspecific hybrids were published by Lemaire (1863) and Verschaffelt (1863). More recent successes were reported by Adele Grant (1924), McMinn (1951), Vickery (1956), and Lenz (1956). McMinn's breeding program was quite extensive and involved crossing, selfing, and backcrossing all species. During the course of this study, I was fortunate to be able to observe numerous *Diplacus* hybrids made by Lee Lenz in his horticultural breeding program. Except for crosses involving *D. clevelandii,* the progeny were vigorous and fertile; and these results are therefore comparable with those reported by McMinn. Internal barriers to interspecific hybridization in *Diplacus* have not been demonstrated and are not likely to be present except possibly in the case of *D. clevelandii. Diplacus clevelandii* is likewise the only species in which vegetative reproduction is known.

POLLINATION

The inflorescence is a loose raceme. The flowers have a five-lobed calyx; a narrow floral

tube; didynamous stamens, with the filaments inserted in the tube by pairs; and expanded throat with upper and lower flaring corolla limbs, two- and three-lobed respectively; and a superior ovary which supports a single style with a sensitive, bilamellate stigma, a unique structural adaptation for pollination. The sensitive stigma is not only common throughout this genus but appears also in several related genera of Scrophulariaceae, among a number of genera in Bignoniaceae, and again in Orobanchaceae.

In *Diplacus* the two-lipped stigma, which may be protruded from, or included in, the corolla throat, stands at the tip of the style, which extends along the upper surface of the throat just above the two unequal pairs of stamens. When the stigmatic lips are open and receptive, a tactile stimulus will cause them to close by compressing laterally, thus sandwiching any deposited pollen between the adjacent stigmatic surfaces. The stigma will open again in 20 to 30 minutes.

Two continuous or spotted orange guide lines are marked on the lower surface of the throat and lead to the nectar that is secreted into the tube by the nectaries at the base of the ovary.

TABLE 1. *The approximate climates of six California communities*[a]

COMMUNITY	FREQUENCY OF SPRING FOG[b]	GROWING SEASON[c]	TEMPERATURE[d] RANGE OF MEAN SUMMER MAX.	TEMPERATURE[d] RANGE OF MEAN WINTER MIN.	AVERAGE YEARLY PRECIPITATION[e]
Coastal Sage Scrub	High	Late winter and spring: 9–12 mos.	68°– 90°F	37°–48°F	10 to 20 in.
Chaparral	Low	Late winter and spring: 7–10 mos.	82°– 94°F	29°–45°F	14 to 25 in.
Southern Oak Woodland	Low	Late winter and spring: 7–10 mos.	84°– 92°F	32°–44°F	15 to 25 in.
Yellow Pine Forest	Very low	Late spring and summer: 4–7 mos.	80°– 93°F	22°–34°F	25 to 80 in. Considerable snow
Pinyon Juniper Woodland	Very low	Late spring and early summer: 5–8 mos.	88°– 95°F	20°–30°F	12 to 20 in. Part in snow
Joshua Tree Woodland	Very low	Late spring: 5–9 mos.	95°–100°F	22°–32°F	6 to 15 in. Part in snow

a. Adapted from California Plant Communities (Munz and Keck, in Munz, 1959) and Climate of California (Sprague, 1941).
b. Higher frequency of spring fogs occur along the coast, especially on the coastal headlands.
c. The growing seasons were established according to the number of frost-free days per year. However, aridity is at least equally if not more important in limiting the growing season during the dry fall and summer.
d. Lower temperatures occur in the higher altitudes and latitudes; higher temperatures occur at the lower elevations in the more southern latitudes.
e. Higher precipitations occur in the more northern latitudes and the cismontane sides of the higher mountain ranges.

Upon entering the throat orifice and following the guide-lines, the prospective pollinator brushes against the stigmatic lips and triggers their closing. After passing the stigma, the pollinator's head or back becomes dusted with pollen from the two pairs of anthers. Since the stigma is closed when the pollinator leaves the flower, pollen of the same flower is not deposited effectually on its stigma. It is possible, however, that self-pollination might occur between flowers of the same plant since, on any one plant, a number usually are open and could be visited by the pollinating animal in sequence.

This structural adaptation for outcrossing has become modified for autogamy in *Diplacus calycinus*. Instead of the style exerting the stigma beyond the anthers, the open and receptive stigmatic lips are behind the outer pair of anthers and are slowly pushed into the de-

hisced pollen by elongation of the style. A visit from a pollinator would push the anther pair into the stigma.

The possibility of a growth-rate differential between foreign and self pollen tubes has not yet been established in *Diplacus*. The only other mechanism which might assure cross-pollination is the slight time lag which may occur between the time the stigma is receptive and the slightly delayed ripening of the anthers. In the case of hummingbird pollination, this slight delay may be of particular importance. It is a common morning practice for the birds to pry open the limbs of an opening flower, at which time the stigma usually is receptive but the anthers have not dehisced.

The principal pollen vector for all known species of *Diplacus* is the hummingbird, whose inconsistent behavior on flowers and wide range foraging probably brings about cross-pollination of many interfertile populations within an area. Since the hummingbird has been found visiting members of all kinds of *Diplacus* populations, from the Pacific Coast to the mountain elevations of 7,000 feet and down the desert slopes to the Desert Woodlands, the fact that these *Diplacus* populations have become thoroughly intercrossed is easily accounted for.

There are times when the hummingbird will take possession of and appear to restrict its flight range to the margins of a particular population, perhaps during the height of the entire flowering period; yet, on other occasions, I have seen individuals sweep in suddenly, visit two or three flowers, then dart away over the hill, more interested in a snack, seemingly, than a steady diet.

A flower well-adapted for hummingbird pollination is often described as pendulous, extended away from the vegetative parts of an open-habit plant by a long supporting pedicel, having red or yellow-colored corollas with the stigmas and anthers exerted and the lower corolla lips not extended. This also is a fairly accurate description of the insular *Diplacus parviflorus* Green (= *Mimulus flemingii* Munz) and only slightly less so of *D. puniceus*, the south coast species.

In mixed and segregating populations of *D. puniceus* × *D. longiflorus*, a few individual plants with more or less typical hummingbird flowers often appear among other variants less well adapted. In mixed populations of this type, hummingbirds will visit at least one and perhaps all *Diplacus* of red flowers and then follow up by visiting plants with salmon, yellow, and cream flowers. If the particular area does not contain red-flowered *Diplacus*, then the bird will visit and even defend *Diplacus* populations of any flower color.

In the flowers of certain plants, visual or chemical "empty" signals are triggered or left during visits by their pollinators, a thesis that has been given considerable attention by L. van der Pijl (1954, 1960). Among his extensive observations of *Xylocopa* spp. (Carpenter Bees, which leave chemical "empty" signals) was a particular, admittedly limited, experience which concerned the "picking" of flowers, by a hummingbird, in a population of *Mimulus aurantiacus* Curt. (= *Diplacus aurantiacus* Jeps.). Van der Pijl entertained the possibility that the closed stigma might constitute an "empty" signal to deter repeat visits. At least for hummingbird visits to *Mimulus* and *Diplacus*, this hypothesis is not valid. The following observation is a case in point: On July 7, 1956, at 6,000 feet elevation in Icehouse Canyon, San Gabriel Mountains, I observed a female Anna's Hummingbird, *Calypte anna*, revisit five flowers of *Mimulus cardinalis*, in which, on the previous flight, she had fed and closed the stigmas.

One of the two lesser transmitters of *Diplacus* pollen is a hawk moth, *Celerio lineata*, and possibly other nectar-feeding genera of the same family (Sphingidae). The hawk moth, perhaps, is the most selective of the *Diplacus* pollinators. On two occasions beside the Glendora Mountain Road, east of Mount Baldy Village, San Gabriel Mountains, I observed a *Celerio* repeatedly visit and pollinate the few remaining late flowers in a population of

D. calycinus, while an adjacent and abundant supply of another hawk moth favorite, *Mentzelia laevicaulis,* a species of Blazing Star, went unattended. The frequency of *Celerio* on *Diplacus* may, however, be low, since I have observed hawk moth visits on *Diplacus* only twice despite a large number of attempts to discover them. On the other hand, in Icehouse Canyon, San Gabriel Mountains, I have repeatedly observed *Celerio* visiting *Mimulus cardinalis,* whose flowers seem less well adapted to hawk moth pollination than those of *Diplacus.*

A third vector, the long-tongued cyrtid fly, *Eulonchus smaragdinus,* was observed as a common and effective pollinator of *Diplacus calycinus* in the montane populations of the San Gabriel Mountains, and both of *D. calycinus,* the mimulus-like *D. clevelandii,* and their introgressants, at 4,000 ft. and above in the Santa Ana Mountains. Dr. Richard Straw also collected several specimens of this fly visiting *D. longiflorus* in Cucamonga Canyon, San Gabriel Mountains. Though the proboscis of *Eulonchus smaragdinus,* which is rigid and carried back between the legs, seldom exceeds 14 mm in length, and the slender tube of *D. calycinus* varies between 27 mm and 39 mm, the nectar rises sufficiently high to be obtained by this insect, at least during the early morning. The length of its proboscis is quite adequate, however, for successful visitations to the flowers of *D. clevelandii,* with their shorter tubes, at any time. On several occasions, I have observed *Eulonchus smaragdinus* sleeping in the floral throat of *D. calycinus* overnight—a behavior paralleling that of the *Pseudomasaris* wasps which pollinate *Penstemon spectabilis* (Straw, 1955). This behavior might insure the short-tongued individual of an early diurnal food supply, a fact which might be of importance, since hummingbirds were visiting the same populations and therefore in competition with *Eulonchus* for the nectar.

SEED DISPERSAL

Very little is known concerning seed dispersal in *Diplacus.* Normally, large numbers of tiny seed are produced in numerous capsules that dry and dehisce, when mature, along a single suture on the upper surface. The seeds remain in this boat-like container beneath placental valves until they are scattered by some sort of disturbance, the most likely agent being the wind. The capsules begin to dehisce during late spring and continue sometimes into the middle of the summer. During this period it is not uncommon for local whirlwinds, called dust-devils in the desert, to move through, picking up and scattering much larger and heavier objects than *Diplacus* seed. If seed remains in the capsule until the fall season, the Santa Ana winds are certain to complete the broadcasting, this time in a southwesterly direction.

Diplacus seed germinates quickly and easily. If, however, the germination of coastal seed is compared to that of the inland seed, e.g., Point Loma and La Mesa populations, the latter germinates over a longer period of time and thus may contain a delayed germination mechanism.

CYTOLOGY

Because I found low pollen fertility in some transplants and wanted to check previous chromosome counts, I examined the fertility of pollen and the meiotic divisions of PMC's mostly from plants within the immediate area of investigation.

Pollen grains from at least 10 specimens per population (5 plants of *D. aridus* and 1 transplant of *D. aurantiacus*) were stained with cotton blue and lactophenol. I scored at least 500 grains per specimen.

The PMC's were fixed in a 2:1 solution of distilled water and propionic acid saturated with iron. This is a slight modification of the fixative recommended for *Mimulus* by Mukherjee, Wiens, and Vickery (1957), who use either acetic or propionic acid. Permanent squashes were made in propionic carmine and Hoyer's medium (Beeks, 1955). Because

of the problem of cytoplasmic staining, the above fixative has proved successful for several other genera of Scrophulariaceae, e.g., *Scrophularia* and *Penstemon*.

McMinn (1951) reported chromosome numbers for *Diplacus aridus, D. calycinus, D. clevelandii, D. fasciculatus, D. puniceus,* and *D. longiflorus* × *D. clevelandii* to be n = 10. He further reported that the pollen fertility of all field entities, except *D. clevelandii,* was 90% or better.

I examined the meiotic divisions of PMC's in *D. aridus,* Jacumba, San Diego County; *D. calycinus,* Toll Camp, San Bernardino Mountains, San Bernardino County; *D. longiflorus* (=*D. australis* McMinn and *D. longiflorus* var. *linearis* Munz), Lakeside, Cuyamaca Mountains, San Diego County; *D. longiflorus,* Thompson Creek, San Gabriel Mountains, Los Angeles County; *D. puniceus,* La Mesa, San Diego County; *D. aurantiacus,* transplant from Fort Bragg, Mendocino County. For all examples, meiosis appeared normal, and the chromosome numbers were n = 10 consistently. Vouchers for these counts are deposited in the writer's herbarium.

Pollen samples of the above populations and the *D. aurantiacus* transplant were 85% to 100% fertile. The fertility of the transplants showed a wider variability, however; it appeared to be correlated with the general health of the plant or out-of-season flowers. The pollen of one plant of *D. calycinus* varied between 40% and 100% fertility.

METHOD OF POPULATION ANALYSIS

The original plan of analysis required the measurement of 25 plants selected at random from each population. Subsequently this number was increased for statistical reasons to 30. For comparison, collections and measurements were made in the areas between and beyond the populations first analyzed. Because many features of the *Diplacus* flower are lost in the press, each individual was measured and recorded on a uniform data sheet in the field. Selected individuals were transplanted to the experimental garden and observed critically during successive years. A number of populations were near enough to allow periodic visits throughout the year. The transplants from these were compared with the individuals remaining in the natural habitat. Many populations were revisited and measured two or more times.

All *Diplacus* taxa were grown in the experimental garden from field transplants, except *D. parviflorus,* whose variable seedlings were grown by the Rancho Santa Ana Botanic Garden from Santa Cruz Island seed collected by Mr. E. K. Balls.

The morphological features chosen for analysis are listed and described in tables 2 and 3. Since the vegetative characteristics were variable in expression, the more constant reproductive structures were used for analysis. Many of them, e.g. calyx shape, pubescence, and pedicel length, have been utilized by other *Diplacus* systematists, while some, e.g., corolla color scoring and tube length, are innovations introduced here. The orifice and the tube curvature evidently have not been utilized previously.

Color was scored by selecting a series of newly opened flowers from plants growing in the experimental garden, which exhibited the known color spectrum of *Diplacus.* They were compared with the colors in the Nickerson Color Fan under standard conditions of illumination. The selected colors of the fan were then used for comparison in the field. There are some variations in the lighter creams which could not be segregated by this method of color indication; however, this end of the spectrum was not critical to the investigation.

In the Laguna Series, 11 populations were selected to represent, graphically, the themes which had been indicated in the analysis of the entire series. Pictorialized scatter diagrams and hybrid indexes, as prescribed by Anderson (1949, 1954a, 1956, 1957), are found in fig. 8–19 for each of the 11 populations. For 8 of the 11 populations, the hybrid indexes

are combined with the important geographic profiles of the Laguna Series (fig. 20). In fig. 21, the range of variation, the mean, and the standard deviation from the mean are calculated for the pedicel-length tube-length difference, and correlated with the percentage color distribution for each of the 16 populations in the Laguna Series and 3 in the San Diego Series. The general morphological mode and distribution for 11 populations in the Laguna series and 3 from the San Diego Series are shown, in fig. 22, by metroglyphs placed on an area map (Anderson, 1957).

TABLE 2. *Morphological characteristics utilized in the analysis of populations*

CHARACTERISTIC	DESCRIPTION OF CHARACTERISTIC
Tube and pedicel, difference between	The slender, neck-portion of the tube is measured from the tube base to the nearest indentation point of filament insertion.
Tube angle	The curve of the tube varies from a slight upward, or recurved, position to a decided downward angle. The angle is measured to the nearest five degrees.
Calyx shape	The opposing extremes of calyx shape were established. The ranges of these extremes were restricted; thus the range of variation in the intermediate category is broad.
Calyx vestures	The density of epidermal hairs varies from glabrous to matted. At least three kinds of hairs are involved: simple, branched, and glandular. Narrow extremes and a broad intermediate class, which included both quantity and quality, were established.
Throat orifice, difference between height and width	The height of the throat mouth was subtracted from its width.
Corolla color	A comparative color scale was established by using the Nickerson Color Fan[a] (Wright, 1958).
Plant habit	The relative height, decumbency, and compactness were compared. The degrees of annual sprouting from the basal crown and the absence of permanent, major stems is important.

a. Munsell Color Company, Inc., Baltimore 2, Maryland.

RESULTS OF POPULATION ANALYSIS: LAGUNA SERIES

The Laguna Series of population is in part a perplexing and complex array of variants, hybrid swarms, clinal gradients, and disturbed habitats. Also existing within this series, however, are relatively stable habitats housing uniform *Diplacus* populations. For the sake of clarity I shall first describe three of the more uniform species populations, two representing the taxonomic and geographical extremes and the third intermediate between them. The population, the habitat type, and the *Diplacus* species it contains are presented in the subsequent order: (1) Temescal, Temperate Hillside habitat, *Diplacus puniceus* (fig. 2); (2) Toll Camp, Rock Crevice habitat, *D. calycinus* (fig. 3); (3) Thompson-Sage, Insolated Hillside habitat, *D. longiflorus* (fig. 4). Following the above descriptions, I shall analyze the populations as they exist within and between the mountain systems in the Laguna Series.

TEMESCAL

This population of *Diplacus puniceus* (fig. 9) was selected in the Santa Ana Mountains near the summit of San Juan Pass west of Lake Elsinore. The local distribution includes the lower northeast slopes of the Santa Ana Mountains above Temescal Canyon wash. Additional population samples of this species were taken as far north as Indian Canyon, south to the base of Palomar Mountain and at various locations along U.S. Highway 395 to Escondido.

D. puniceus competes in the Coastal Sage Scrub, open or low Chaparral communities, and their ecotone. The species also appears along the margins of thick Chaparral and occa-

TABLE 3. *Comparison of the morphological characteristics and habitats of Diplacus puniceus, D. longiflorus, and D. calycinus*

CHARACTERISTIC	*D. puniceus*	*D. longiflorus*[a]	*D. calycinus*
Plant habit	Tall, erect; a few permanent, major stems from the crown.	Tall, procumbent; a few permanent, major stems from the crown.	Short, procumbent; diffuse, annual sprouting from the crown.
Corolla color (see color wheel, fig. 21)	Bronze to red; occasionally near-orange.	Salmon-orange with occasional reddish variants.	Creams: white to golden.
Tube length	Short: 6–16 mm	Intermediate: 13–27 mm	Long: 27–39 mm
Pedicel length	Long: 10–39 mm	Short: 2–11 mm	Short: 2–11 mm
Throat orifice	Taller than wide; smaller area.	Height and width near-equal; larger area.	Wider than tall or equal; larger area.
Tube angle	Strongly curved; range 15°–35°.	Moderately curved to straight; range 0°–20°	Moderately curved, straight or recurved; range 0°–15°
Calyx shape	Short, angled; throat not inflated.	Varies between *D. puniceus* and *D. calycinus.*	Long, not angled; throat inflated.
Calyx vestures	Sessile, resin producing glands; no hairs.	Varies between *D. puniceus* and *D. calycinus.*	Copious amount of glandular and non-glandular, simple and branched, hairs, and sessile glands.
Habitat	Temperate Hillside: Coastal hills, in Coastal Sage Scrub, but also in low or open Chaparral and their ecotones.	Insolated Hillside: Inland, cismontane foothills; in low or open Chaparral, Coastal Sage Scrub and their ecotones.	Rock Crevice: Inland above 2000 ft.; on rock cliffs or banks, and in granitic boulders and outcrops; desert woodland and mountain communities.

a. San Gabriel Mountain race.

sionally grows scattered in Southern Oak Woodland. In shaded locations a clambering growth habit is assumed by some individuals. One specimen was found climbing up through and to the top of a shrub 8 to 10 feet tall.

The soil of this population is derived from elevated alluvium and, due to its clay, is moderately heavy. Some plants of *Diplacus* are found in decomposed sandstone and other light substrates, but usually these individuals are exposed only to limited amounts of direct insolation.

At maturity, *D. puniceus* is erect, 3 to 5 feet tall, and has a spread of 2 to 3 feet. The branching habit is decussate, usually sparse, with a few major stems ascending from an obscure rootcrown. Though some of the longest stems tend to become decumbent at the tips, in full sun, the plant retains a slender open and upright appearance.

Following the summer-fall dormancy, a majority of the winter and spring growth originates from the previous year's wood. Though usually but few shoots are initiated from the root-crown, a few eventually become established as major stems. The young shoots have anthocyanin in the sun-exposed epidermal layers of the stems. The stems and leaves are glabrous yet glutinous due to a viscid resin produced by sessile epidermal glands.

The inflorescence is an open, decussate raceme, bearing an indeterminate number of long "S"-shaped pedicels each supporting a single flower. The glabrous calyx is glutinous, tubular, plicate, not inflated, reddish-colored from anthocyanin along the upper sun-exposed surface and bent medianly in a downward angle. Included in the calyx is a short, curved floral tube expanding into a throat at the calyx mouth. The corolla throat is equal in length to the tube and has a relatively small orifice, is higher than wide, and incloses a pair of

bright orange, elongated, teardrop-shaped guide-lines pointing to the narrow tube entrance. The broadly lipped stigma and the anterior pair of anthers usually are well-exerted from the mouth of the corolla throat, and the anthers are positioned behind the stigma. The two limbs of the corolla are flared but seldom extended or reflexed. The two upper corolla lobes are notched, the three lower lobes are truncate and entire.

The variation in corolla color ranges from near orange through the bronze-red, red-blush, red-orange, and orange-red to bright scarlet red (fig. 21). The deepest red, Munsell 2.5 R3/7, found in a form of *D. longiflorus ("D. rutilus")*, was not found in any of the *D. puniceus* populations that I sampled. The above color variability results from inherent differences and environmentally induced phenotypic plasticity.

As would be suspected from the floral morphology and corolla color of *D. puniceus*, hummingbirds are the principal pollinators. The exertion of the stigma beyond the orifice eliminates *Eulonchus* as a successful pollen vector. I have not observed or heard of moth visits to this species. Because of the separation of the stigma and the anthers, their exertion from the corolla throat, and the large incidence of hummingbird pollination, I assume that *D. puniceus* is infrequently selfed.

In the hillside disturbances to vegetation and soil *D. puniceus* is usually quick to become re-established. However, there are three conditions which limit its success in open habitats: (1) overgrazing by cattle, (2) steepness of the slope, and (3) fire.

In areas heavily grazed by cattle, *D. puniceus* is absent except in ravines or along roads, banks and fence margins where the cattle are not inclined to travel. This may be due, at least in part, to the species' long brittle stems and its tendency to succumb to chlorosis when submitted to extensive breakage. Also, *D. puniceus* is seldom able to establish more than a very few seedling pioneers on the perpendicular roadcuts and cliffs, apparently because of excessive plant fracturing by winter winds.

D. puniceus seems limited in its ability to recover from brush fires, a common disturbance in Chaparral and Coastal Sage Scrub. Following the summer fire of 1959 in the Ortega-San Jose Pass region of the Santa Ana Mountains, the only surviving *Diplacus* that could be found were either skipped by the fire or crown sprouting in the ravines where the vegetation had been only scorched or partially burned.

Though, in most cases, Temescal *Diplacus* showed average *D. puniceus* features, the population did not represent the potential extremes that were indicated later by the Point Loma population.

TOLL CAMP

Diplacus calycinus (fig. 19) is a common inhabitant in the rock crevices of the granite boulder foothills and ridges of Pinnacle Mountain. The Pinnacle is a semi-arid peak on the desert side of the San Bernardino Mountains, which rises above Toll Camp between the Deep Creek and Grass Valley tributaries of the Mojave River. A population area northwest and adjacent to Toll Camp was selected for this measurement and analysis. Further samples were observed along the Hesperia Road, Cushenberry Grade, Victorville-Lucerne Road near Yucca Valley, at Hidden Rocks in the Joshua Tree National Monument, Little San Bernardino Mountains, and Tye Summit and San Antonio Falls in the San Gabriel Range.

This species is a pioneer in the slow succession of the Rock Crevice habitat. It does not compete directly in the surrounding communities or ecotones of Yellow Pine Forest, Pinyon Juniper Woodland, Chaparral, and Joshua Tree Woodland but, instead, remains isolated and deeply anchored in the fissures of parent rock formations. In the crevice pockets, the limited soil often consists of leached loose mixtures of organics and granite or feldspar residuals. Germination of *D. calycinus* takes place in the bare rock fissures or in the soil pockets, the roots quickly extending into the bare rock fissures well beyond the limits of the soil.

In addition to the summer and early fall dormancy of *D. puniceus*, the growth of *D. calycinus* is suspended also through the cold period of late fall, winter, and early spring. Upon the advent of temperate weather, the species quickly recovers and commences flowering. Each year's new growth originates mostly from a well-developed rootcrown and not

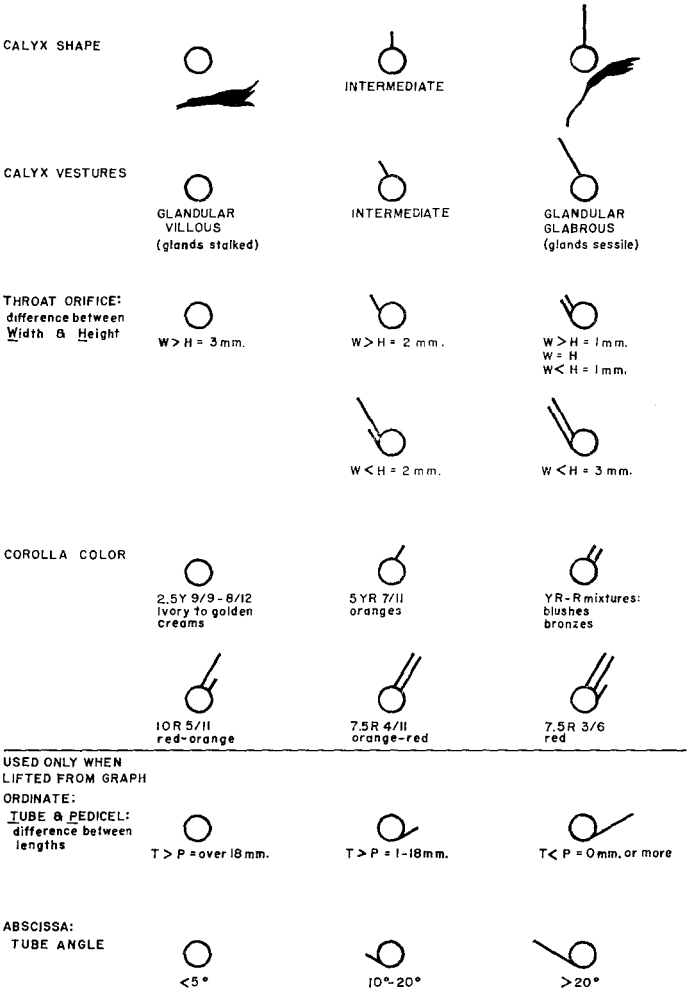


Fig. 7–19.—Morphological features used in population analysis are coded on metroglyphs in fig. 7. In fig. 8–19, the measurements of each plant analyzed are coded on a metroglyph placed in a pictorialized scatter diagram of its population. Each long ray on a metroglyph is valued as two, a short ray as one, no ray as zero. The metroglyph's position, relative to the values on the ordinate and the abscissa, is equal to its ray substitute, as indicated below the line in fig. 7, in which case the glyph is independent of the graph and may be placed on maps, e.g., fig. 22. By totaling the metroglyph rays, the individual's index number is obtained. The index value is placed on a frequency-index histogram with the remainder of the population. The index values are located on the abscissa, the frequency on the ordinate.

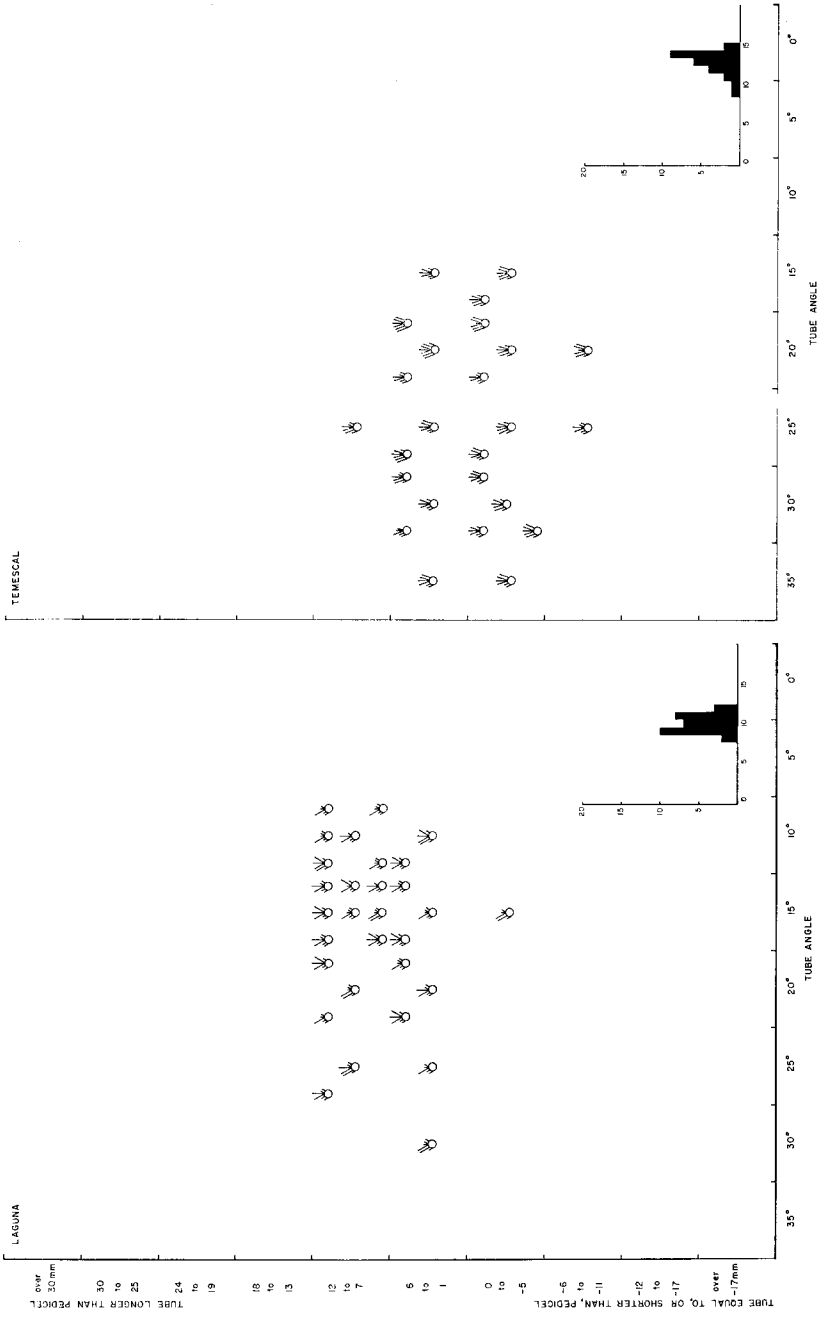


FIGURE 8

FIGURE 9

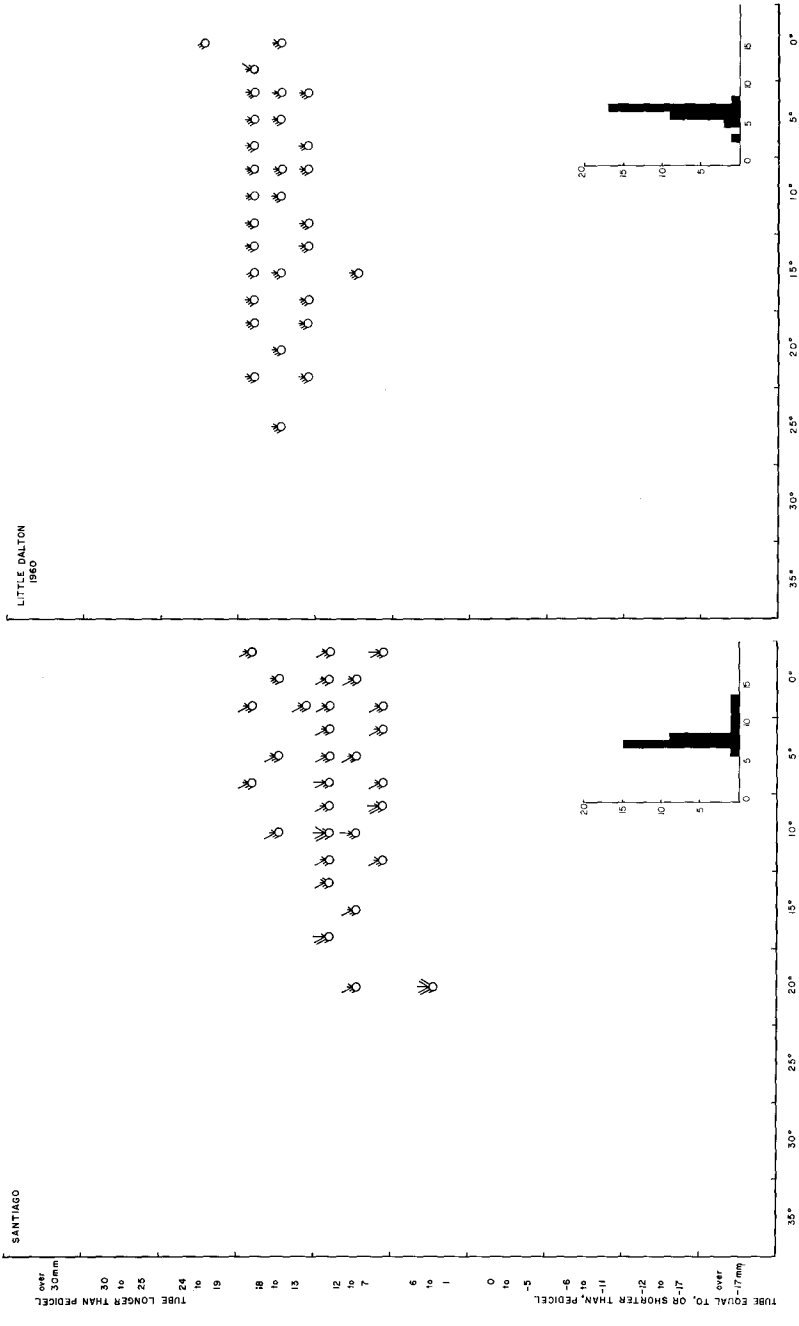


FIGURE 10

FIGURE 11

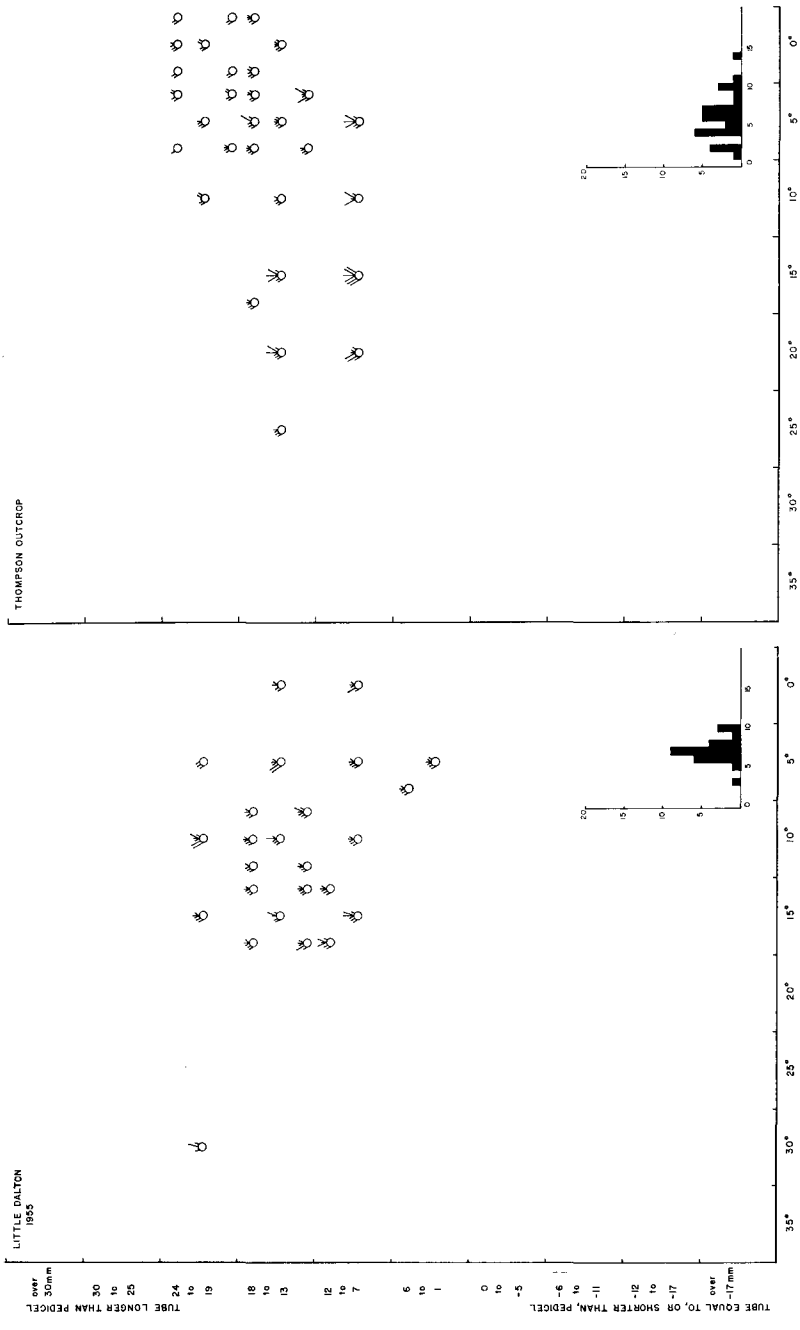


FIGURE 12

FIGURE 13

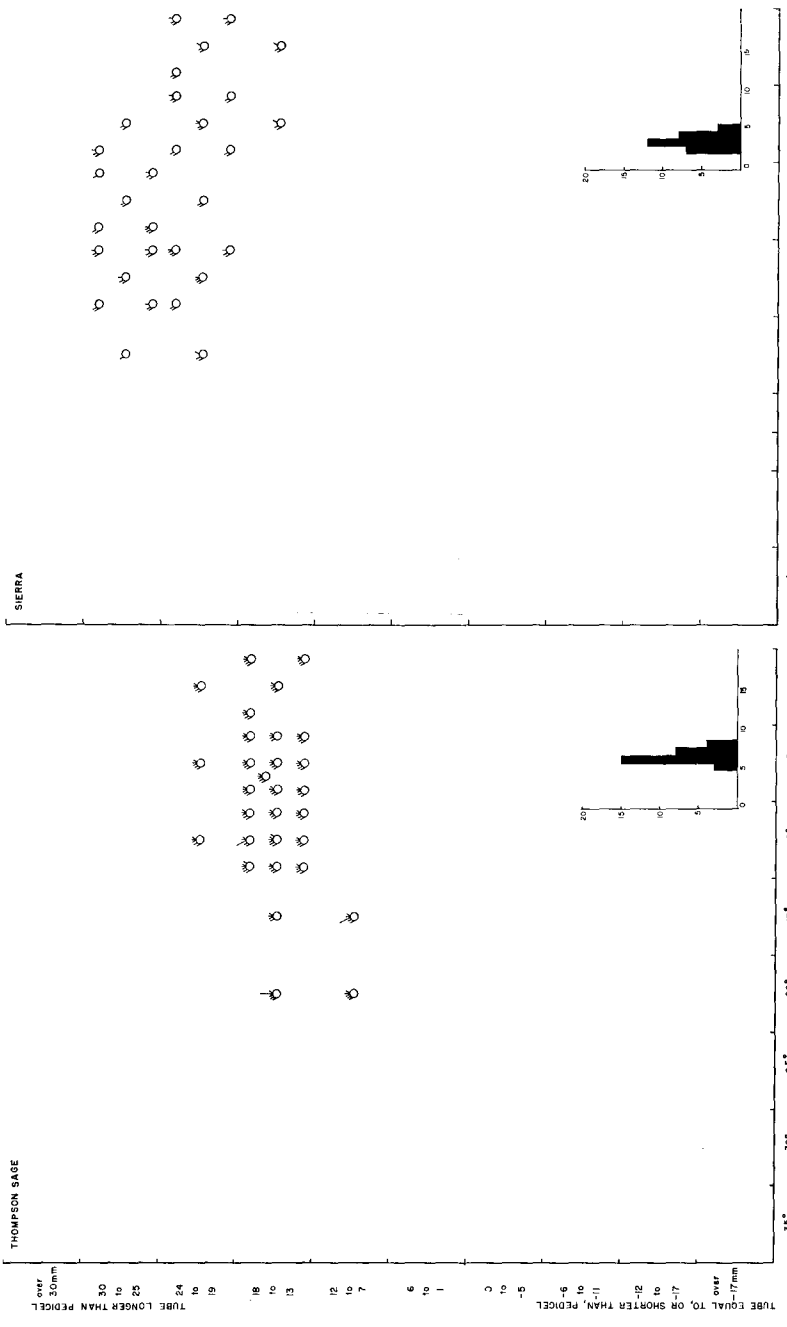


FIGURE 14

FIGURE 15

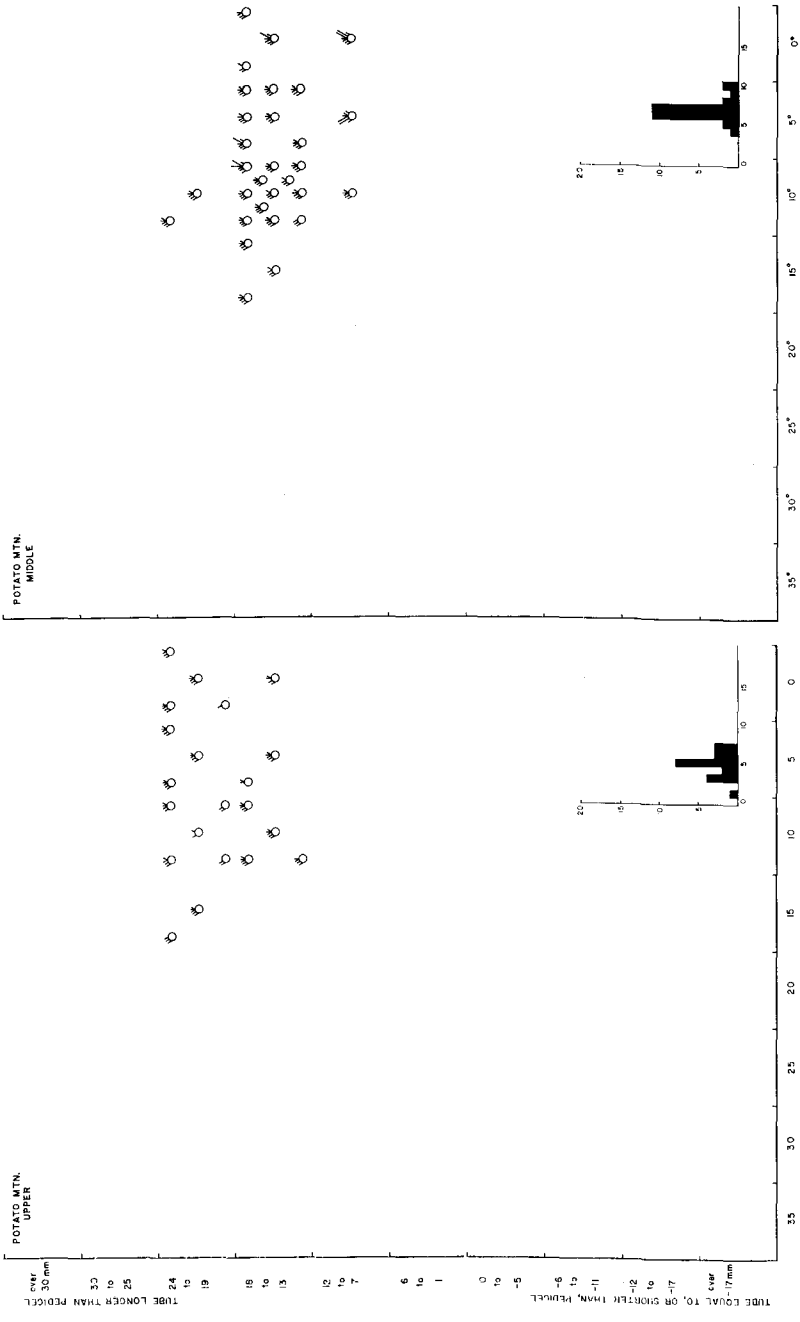


FIGURE 17

FIGURE 16

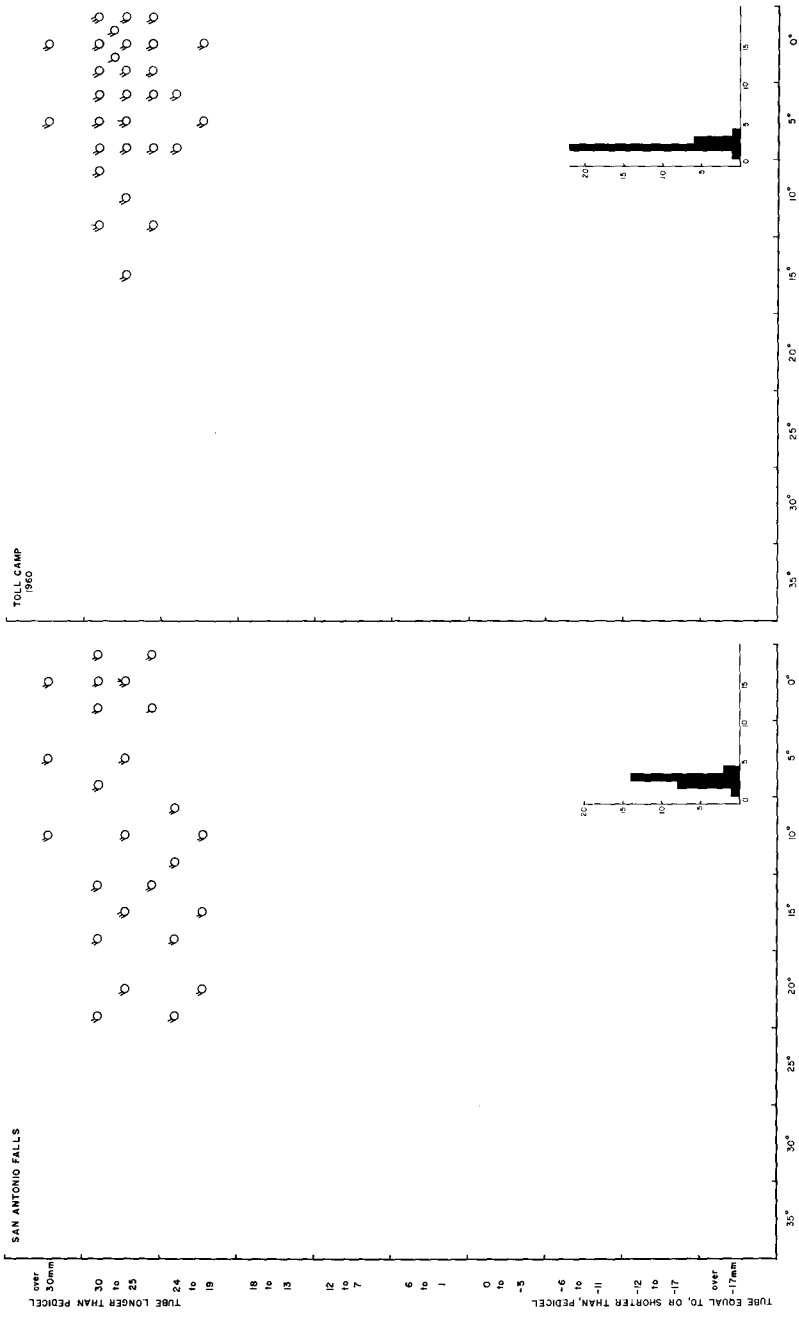


FIGURE 18

FIGURE 19

from the previous year's wood. The *D. calycinus* habit is diffuse becoming decumbent, sometimes radiating or cascading 3 or 4 feet from the crown. The young stems are greenish-white and lack the anthocyanin found in *D. puniceus.* The young shoots and the underside of the leaves are villously clothed by simple and branched hairs commonly gland-tipped. The upper leaf surface is glutinous and nearly glabrous.

The racemose inflorescence is more compact than in *D. puniceus,* with the pedicels much shorter and densely glandular-villous. The calyx is similarly pubescent, tubular in the lower half, and then abruptly expanded into an inflated throat. Each corolla has a long, straight narrow tube which also abruptly expands to a throat. The length of the *D. calycinus* throat is about one-half the length of the floral tube but at least equal to the throat of *D. puniceus.* The width of the throat orifice is at least as great, and often greater, than is its height. The orifice area is larger than that of *D. puniceus.* The guidelines are mostly continuous and teardrop-shaped as in *D. puniceus* but of a lighter orange color intensity. The stigma and anthers usually are included in the throat with the outer pair of anthers sometimes positioned ahead of the stigma. The stigmatic lips, especially the lower, are longer and narrower than in *D. puniceus.* The corolla lobes usually are flexed, rarely extended or reflexed, but in some desert locations are nearly rotate (compare San Bernardino Mountain populations).

Neither red nor orange pigments are present in the corolla of this species. The color variation is confined to three different intensities of pastel yellow, ivory, lemon, and gold. The Munsell color hue of 2.5 yellow is comparable to the highest yellow saturation. Climate fluctuation does not seem either to alter the production or reduce the intensity of the pigment as in the red hues of *D. puniceus.*

In this particular population the only pollinator I have observed is the hummingbird. However, in other *D. calycinus* locations visits by *Eulonchus* and *Celerio* were noted. All three are believed to be effective; however, the hummingbird is commonest. In the *D. calycinus* populations, antogamy is common due to the delayed elongation of the style pushing the open stigma into the outer pair of anthers.

Because of its ability to crown sprout, *D. calycinus,* unlike *D. puniceus,* can withstand extensive amounts of damage to its branching system. It is subjected to ice, snow, and high wind velocity and therefore considerable breakage during a typical winter in the Yellow Pine community. In desert locations, the annual growth is killed by the combined heat and dryness resulting from the summer insolation. The crown-sprouting behavior of this species surmounts both of these obstacles by supplying a new aerial system each year from a protected root system.

This growth adaptation also is an answer to the fire problem for *D. calycinus.* During July, 1959, I watched the Pinnacle Mountain vegetation and the Toll Camp *Diplacus* population burn to the ground in a raging 12,000 acre brush and forest fire. Of the 25 plants, 7 were bulldozed out in a fire break and 18 were burned to the ground. The following May, 1960, all 18 had recovered completely, were flowering and appeared more vigorous than before the fire. Neither the bulldozed nor the burned area showed any re-establishment by seedlings.

THOMPSON SAGE

Diplocus longiflorus (fig. 14) is a very common competitor in the vegetation covering the highly insolated cismontane foothills of the San Gabriel Mountains. The Thompson-Sage population north of Claremont portrays the features of this San Gabriel race and is one of three populations located above Thompson Creek Wash in the extreme southeast corner of the Johnson Pasture foothills. These foothills are low extensions adjacent to the main San Gabriel elevation and occurring approximately two miles west of the mouth of San Antonio Canyon. The total area studied in the San Gabriels traversed the Insolated Foothill habitat of the cismontane slopes from Angeles Crest Highway above La Crescenta,

Los Angeles County to Cajon Pass, San Bernardino County. Within the San Gabriels, eight populations were treated by a full analysis and 12 more were check-sampled.

In the more stable communities of Coastal Sage Scrub, low or open Chaparral and their ecotones, the competing populations of *D. longiflorus* are very uniform. This is only true if the habitat remains closed, and the level of community competition is high. If disturbance or other factors open the habitat, the variation of *D. longiflorus* suddenly increases.

The cismontane foothills are somewhat heavy residuals of metamorphic and volcanic origins. The reddish soil at Thompson-Sage is a mixture of ancient, elevated alluvium and recent feldspar residuals.

As a seedling, the branching habit of *D. longiflorus* is erect and robust but later elongation causes the heavy stems to decline and become decumbent. Though the undulating stem may extend 5 feet from crown to tip, the plant height seldom exceeds 3 to 4 feet unless the plants receive additional support from adjacent shrubs. At maturity, *D. longiflorus* becomes a soft wood subshrub with a half-dozen or so stout major stems freely branching into a complex interwoven superstructure. As in *D. puniceus,* the majority of new annual growth originates from the previous year's wood and not from the root crown.

Depending upon the nearness of *D. calycinus,* the pubescence varies from villous to near-glabrous. Since *D. calycinus* exists at the higher elevations along the entire range, most members of the San Gabriel race of *D. longiflorus* are quite pubescent. The glabrous ones are found along the lower headlands and hills radiating away from the range. As in all *Diplacus,* the foliage is very glutinous and distinctly aromatic.

The inflorescence of *D. longiflorus* is equal in length to that of *D. puniceus,* but due to the short pedicels, villous pubescence, and large flowers, it appears heavier and more compact. The calyx is large, often pubescent, and has a somewhat expanded throat like that of *D. calycinus.* Because the calyx is long and the corolla tube length is intermediate, the floral tube usually is included in the calyx as in *D. puniceus.* The lesser angle of the tube, the shape and size of the orifice, approximates that of *D. calycinus.* The size of the *D. longiflorus* flower, though variable between *D. puniceus* and *D. calycinus,* is often larger than either of these species. The extended lower corolla limb and the laterally reflexed lobes of the upper limb are common but not constant features. Neither of these charactristics is found in *D. calycinus* or *D. puniceus.* The anthers occur in unequal pairs mostly behind the included stigma. The throat guide-lines are mostly continuous, varying in color intensity from deep to light orange. The corolla color also is salmon-orange, Munsell hue 5YR, and of variable intensity. Typically, anthocyanin is not present in either the flowers or the stems.

With the stigma included in the corolla throat, all of the *D. calycinus* pollinators are potential vectors. Of these, I have observed the cyrtid *Eulonchus smaragdinus* and two hummingbird species, Costa's, *Calypte costae* and Anna's, *Calypte anna.* I have not detected visits by hawk moths though they probably occur.

As in *D. puniceus* and *D. calycinus,* outcrossing is prevalent. However, automatic auto-

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Fig. 20.—Shown are the inland and elevational effects on *Diplacus* populations. At the bottom is a profile of the Laguna Series from the Pacific Ocean to San Antonio Peak. The San Gabriel Range is enlarged above. Inset is a topographical map with the two transects of the total profile and the *Diplacus* populations indicated. Also shown are silhouettes of plant habit, pedicel and calyx, and corolla for (a) *D. calycinus,* (b) *D. puniceus,* and (c) *D. longiflorus.* Laguna is less typically *D. puniceus* than Temescal due to a north to south coastal gradient in the former and the protected northeast side of the Santa Ana Mountains in the latter. Santiago Canyon is *D. longiflorus* skewed toward *D. puniceus.* San Antonio Falls is typically *D. calycinus;* because of a lower altitude, the Sierra Sub-station is less typical. Upper Potato exhibits *D. calycinus* tendencies; Middle Potato shifts in the opposite direction toward *D. puniceus.* Thompson Creek Outcrop (1960) exhibits both tendencies. Thompson Creek Outcrop is an open habitat that is geologically caused; Potato Mountain is disturbed by wind and cold at the top and the native fauna at the center.

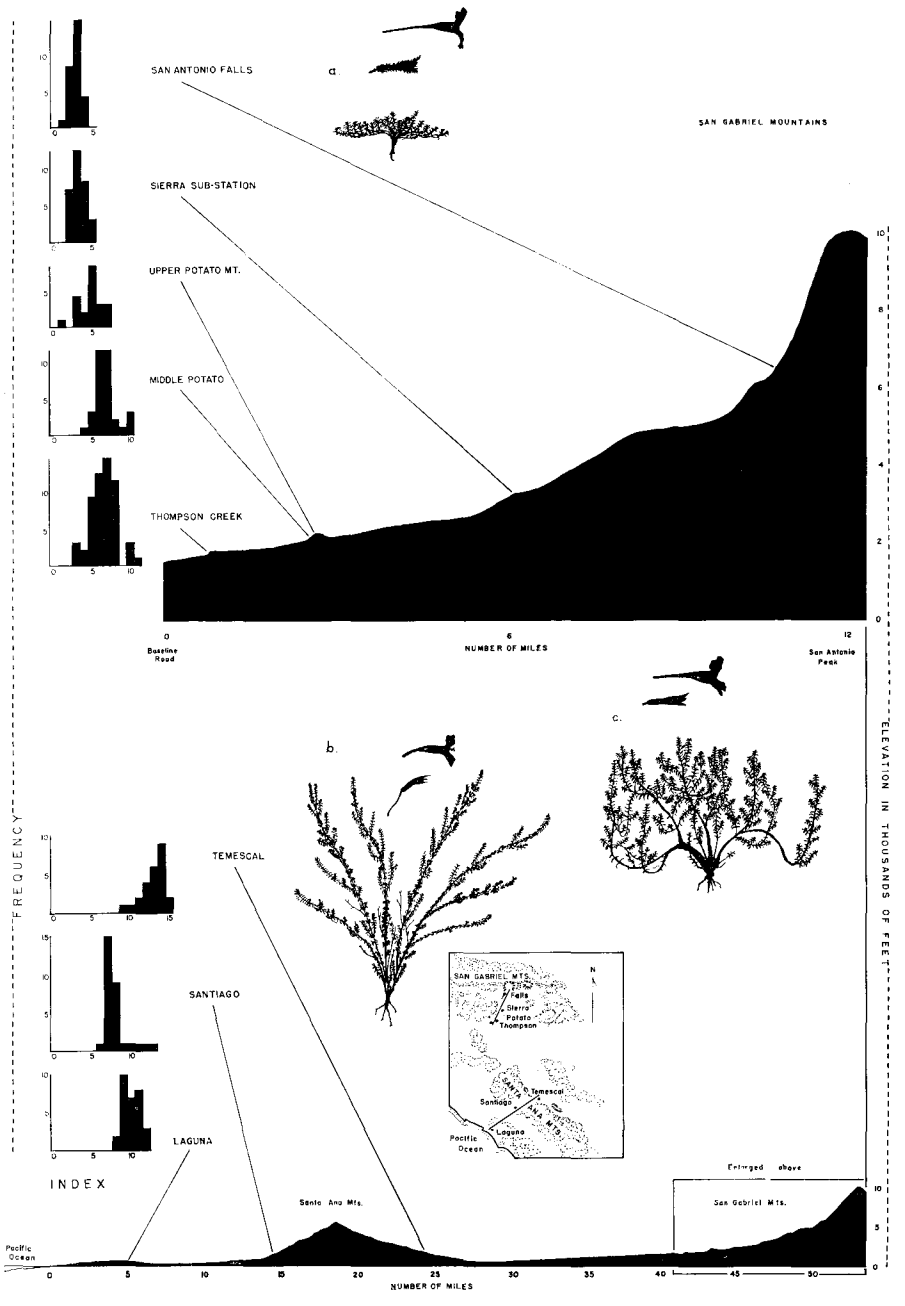
SAN ANTONIO FALLS
SIERRA SUB-STATION
UPPER POTATO MT.
MIDDLE POTATO
THOMPSON CREEK
SAN GABRIEL MOUNTAINS
Baseline Road
NUMBER OF MILES
San Antonio Peak
ELEVATION IN THOUSANDS OF FEET
FREQUENCY
TEMESCAL
SANTIAGO
LAGUNA
INDEX
a.
b.
c.
SAN GABRIEL MTS.
Falls
Sierra
Potato
Thompson
Temescal
Santiago
Laguna
SANTA ANA MTS.
Pacific Ocean
Santa Ana Mts.
Enlarged above
San Gabriel Mts.
NUMBER OF MILES

FIGURE 20

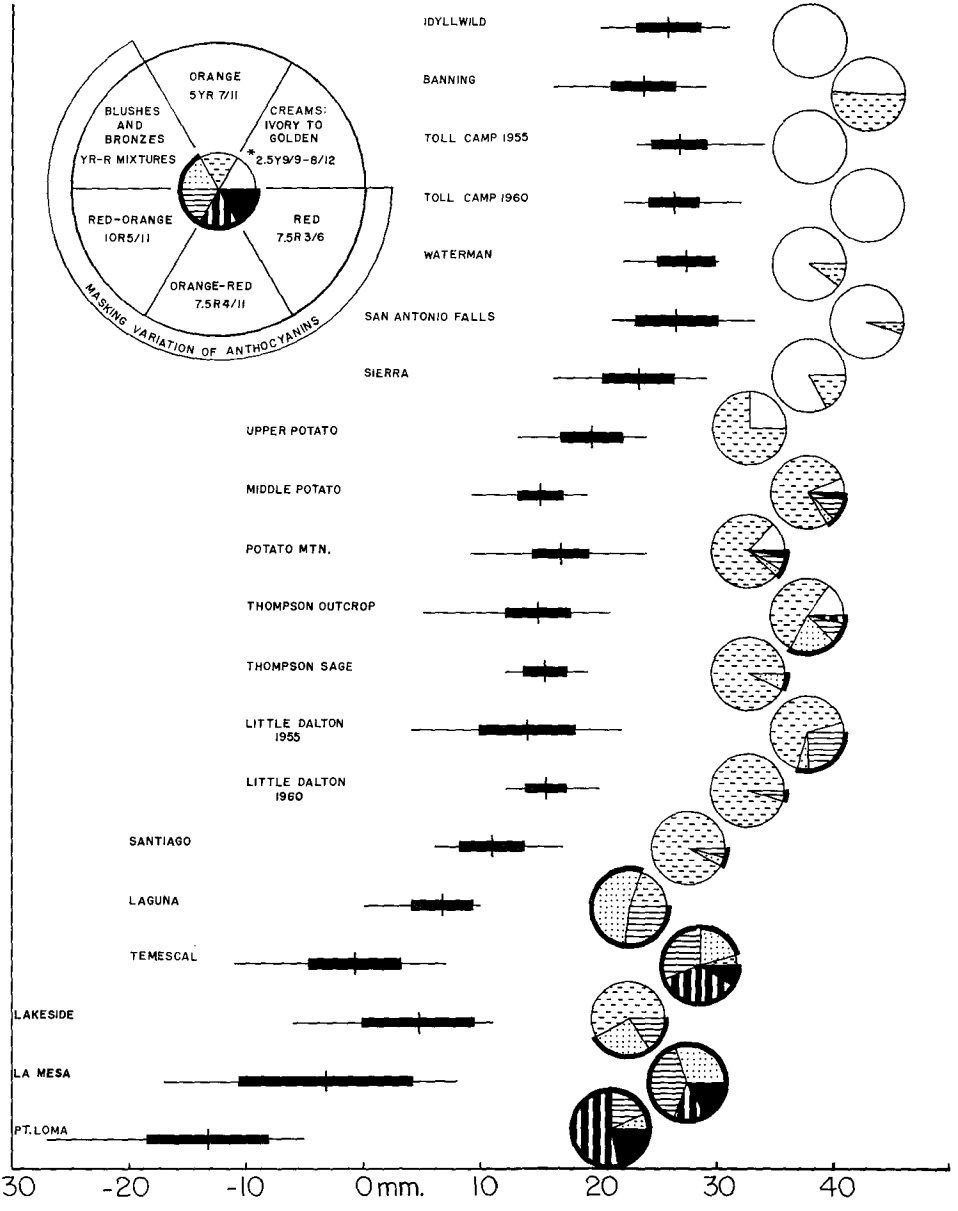

Fig. 21.—Pie-graph and population-range diagrams of color and tube-pedicel length differential. Population samples are arranged from the coast, inland in two series: Point Loma to Lakeside—the San Diego Series; from Laguna and Temescal to Idyllwild, Toll Camp and San Antonio Falls—the Laguna Series. The pie-graphs show the relative percentages of color in each population; the black peripheral band expresses the total occurrence of red. The population-range diagram expresses the variation in the difference between tube length and pedicel length. In each population, the thin horizontal line indicates

gamy may occur infrequently since in several specimens the stigma was held behind the outer pair of anthers.

In the Insolated Hillside habitat disturbances to soil and vegetation are numerous. Though the San Gabriel foothills have not been subjected to grazing, considerable disturbance has been produced by the numerous roads, power-line rights-of-way, firebreaks, earth-fill dams, and scattered mining activities. The natural, precivilization disturbances still present include animal trails, pocket-gopher hills, pack-rat nests, water-eroded ravines, and weather-bared outcrops. Much of the variability found in the *Diplacus* populations of the San Gabriel foothills can be traced to these disturbed areas. However, where disturbance includes the continual shattering of plants, *Diplacus longiflorus* is absent.

Though brush fires in this habitat occur regularly, none of the *D. longiflorus* populations that I have analyzed has subsequently burned. I have checked a number of burned areas which were known to have contained *Diplacus* before the fire. However, I have yet to find plants of *D. longiflorus* that are crown sprouting after they had burned to the ground.

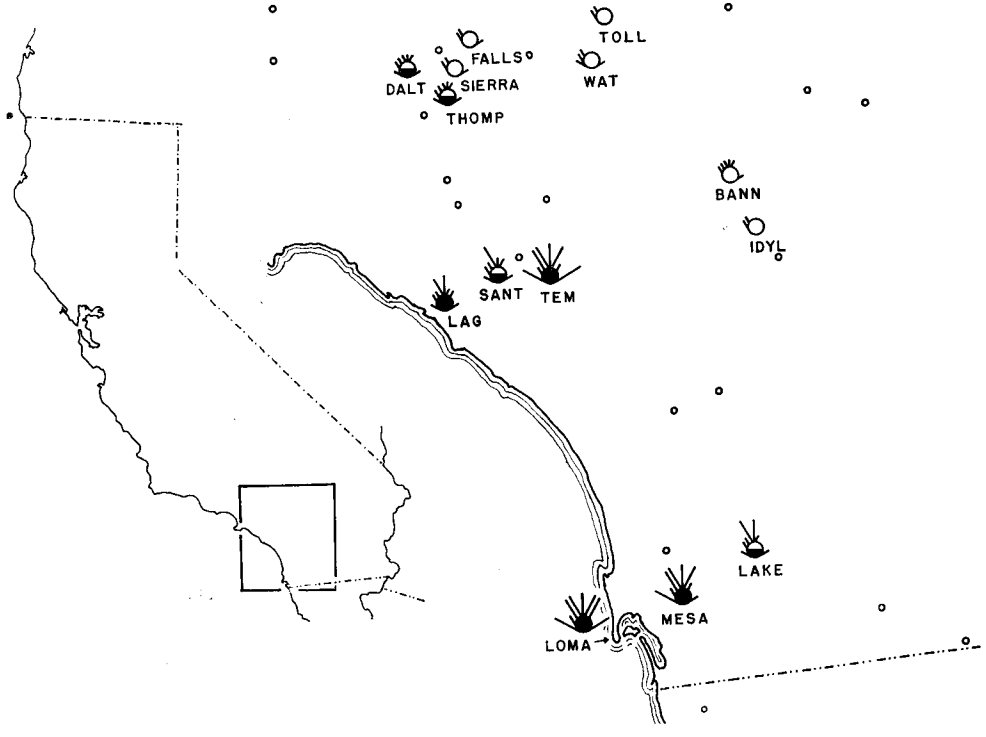

Fig. 22.—The population modes as represented by metroglyphs. The open glyphs represent the *Diplacus calycinus* habit as seen in (a) of fig. 20; the black glyphs, *D. puniceus* as in (b); and the half and half glyphs, *D. longiflorus* as in (c). The small circles represent other populations sampled. (For explanation of glyphs see fig. 7).

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the total variation of the sample; the broad line, one standard deviation from the mean; and the short, vertical cross bar, the mean. For more population data see table 4.

SAN GABRIEL MOUNTAINS

The Little Dalton population occupies an Insolated Hillside habitat on a south-facing slope above Little Dalton Canyon, elevation 2,250 feet. The original 1955 population (fig. 12) was selected as an example growing in a closed habitat of rather stable Coastal Sage Scrub and Chaparral. However, when the measurements were later compared with those of other San Gabriel populations (fig. 12–13), the range of variability was far greater than could be expected for closed community populations and equal to those in the open habitats. Because of this irregularity, I again measured the population in 1960 and found several changes had taken place. During the summer of 1959 a brush fire had burned up to a firebreak bordering the southern limits of the population. In the process of fighting the blaze, fire crews widened the firebreak approximately 10 feet and eliminated most of the *D. puniceus*-like extremes recorded in 1955. Further investigation showed the firebreak to have had a history of periodic widening and subsequent narrowing by vegetative succession along its margins. Apparently, the *D. longiflorus* recombinants were a part of a rapid reentry by Coastal Sage Scrub. Being perennial, some of the *D. puniceus* types were able to remain while the vegetation regained its stability.

In the center of the population, an island of red variants emanated from a different kind of disturbance, a woodrat nest. Growing from the nest was a bright red flowering *Diplacus;* along a short radius from the nest the flower color of the surrounding *Diplacus* graded from red to salmon-orange. Except for a few other human disturbances on the perimeter, the remainder of the 1960 population was very uniform (fig. 11).

The Thompson Creek population occurs at 1,750 feet elevation in an Insolated Hillside habitat on a south-facing, foothill slope two miles west of San Antonio Canyon. Because of its variability, I divided this *D. longiflorus* population laterally into three subpopulations inhabiting three adjacent but different ecological niches: (1) *Sage* on the west, (2) *Outcrop* on the east, and (3) *Chaparral* between the two. Each niche occurs on a shoulder between shallow ravines draining a low ridge.

The habitats are similar climatically but different edaphically. Outcrop is a bare feldspar dike of decaying parent rock retaining only scattered shallow pockets of soil. Sage has a shallow covering of soil overlying fractured and decaying parent rock. Chaparral has the deepest soil of the three, though this is still limited.

Vegetationally, Outcrop contains widely spaced plants in early succession. Sage is dominated by Coastal Sage Scrub, particularly White Sage, *Salvia apiana.* Chaparral is a mixture of Coastal Sage Scrub and Chaparral.

The range of *Diplacus* variability in both Sage and Chaparral is narrow and comparable to Little Dalton 1960. Because these two populations are similarly uniform, I am selecting Sage to represent both (fig. 14). The description is given above.

In the shallow ravine between Chaparral and Outcrop was one red-flowered individual. On the Outcrop side of this ravine, I found an increasing number of red recombinants mixed with the Chaparral vegetation bordering the west side of the feldspar dike.

Outcrop contained the most variable population I have analyzed. On a hybrid index scale of 1-17 the Outcrop *Diplacus* ranges from 1-14 (fig. 13), i.e., from the morphological extreme of *D. calycinus* to the mean of *D. puniceus.* Of the three years this population has been measured, 1957 and 1958 (fig. 13) exhibited the more extreme plants probably because the 1960 population (fig. 20) was decimated by spring heat, Santa Ana winds and drought. Out of a total of 116 plants, only 55 were measurable. The other 61 were either not flowering or dead. Most of the extremes that I had observed earlier in the spring apparently were among those that succumbed to the adverse climate. Further observations of this interesting situation are planned.

The Potato Mountain population is found on the south slope and terrace of a foothill to

Potato Mountain, elevation 2,450 feet. Potato is similar to Thompson Creek except the environment and population differentials range vertically rather than horizontally. (1) *Lower Potato* is an ancient terrace at the base of the hill, (2) *Upper Potato* occurs just below the summit, and (3) *Middle Potato* is approximately one-third of the distance from the terrace to the summit (fig. 16–17, 21).

Chaparral is the dominant vegetation on Lower Potato and Coastal Sage Scrub covers both Middle and Upper Potato populations. Of the two communities, Chaparral offers the greater climatic protection for *Diplacus*. Though Potato Mountain is relatively low, the exposure to air movement and temperature extremes undoubtedly increases with the rise in elevation because of its sentinel-like position at the mouth of San Antonio Canyon.

The soils of Middle and Upper Potato are shallow and highly residual. In numerous places, the decomposing fractured feldspar is exposed on the surface of the slope. Underlying Lower Potato is an ancient terrace of heavy red alluvium that is covered by moderate layers of litter, duff and humus.

Though I observed and photographed the Lower Potato population thoroughly, sudden heat, drought and parched Santa Ana winds dissipated the flowers before any measurements were recorded. The robust habit of the Lower Potato *Diplacus* was typically *D. longiflorus*-like, yet the flowers of numerous plants contained red pigment. This was noticeable in the individuals growing up through the abundant woodrat nests. Of the three Potato Mountain populations, this one is most disturbed by animals, thus providing abundant openings for the invasion of *Diplacus* variants. This habitat also provides the recombinants extra protection from insolation and wind.

A few of the *D. longiflorus* plants of Middle Potato were red-flowered, but the color mode was definitely salmon-orange. Though these *Diplacus* were less robust than in Lower Potato, they definitely dominated much of the vegetation on this slope. The thin soil, steep slopes, exposure to wind, and insolation make the environment of this population much more severe and differently selective than Lower Potato Mountain. Though deer trails and brush rabbit run-ways are plentiful, there are fewer woodrat nests and pocket gopher mounds, and therefore less space available for the establishment of new *Diplacus* recombinants.

A definite shift toward *D. calycinus* takes place at Upper Potato (fig. 16–17, 21). The frequency of the cream color increases, and there were no red-flowered forms. The mean of the flower tube length increases 3 mm over that of the other San Gabriel Mountain *D. longiflorus* populations. Also there is a tendency toward weak stems and smaller habit. More of the disturbance is physically caused by the steepness of the slope, climatic exposure to the wind and insolation, and less is due to gross animal activity.

The *D. calycinus* in the Sierra population occurs on the lower east wall of San Antonio Canyon at an elevation of 3,200 feet. It is a steep Rock Crevice habitat partially shaded by riparian woodland. The parent rock is badly fractured and decayed, thus giving rise to steep talus slides and precipitous gullies. The *Diplacus* are mostly weak-stemmed and cascading from root crowns deeply anchored in the rock crevice; none are growing in the adjacent Chapparral areas. Of 30 individuals, 5 have light salmon-orange flowers, the remainder are creams. The tube length mean increased over Upper Potato by 6 mm but remained nearly 3 mm below that of San Antonio Falls (fig. 20). Though Sierra exhibits a few features typical of *D. longiflorus*, the plants are decidedly *D. calycinus* (fig. 15, 20–21).

I measured another *D. calycinus* population in a Rock Crevice habitat near the San Antonio Canyon Falls at 6,400 to 7,000 feet elevation. The massive elevated blocks of crystalline parent rock are extensively fractured, thus producing deep fissures in sheer cliffs and vast talus slides. Within these crevices and slides, the *Diplacus* grow in shallow soil. As in the Sierra population, the plants were weak-stemmed, but instead of retaining a cas-

cading habit, winter breakage caused a more compact diffuse shape. The flower color was uniformly cream, except for one orange seedling. The tube length increase over the Sierra mean was 3 mm (fig. 18, 20–21).

SAN BERNARDINO AND LITTLE SAN BERNARDINO MOUNTAINS

In the analysis of measurements, *Diplacus* growing on the cismontane slopes and montane divide in the Rock Crevice habitats of the San Bernardino Range compared well with those occurring in similar environments of the San Gabriel Range, e.g., Waterman, 3,000 feet elevation, equals Sierra, 3,200 feet elevation, San Gabriel Range; Strawberry Peak (unrecorded) 6,000 feet elevation, equals San Antonio Falls, 6,400 feet elevation, San Gabriel (fig. 21).

In the Insolated Hillside habitat, *Diplacus* is virtually absent. Though a few orange-colored forms of *D. calycinus* grow on and near the roadcuts and other rock cliffs, I found none competing in the open Chaparral and Coastal Sage Scrub communities on the cismontane foothill slopes.

In the Rock Crevice habitat of the desert slope, *D. calycinus* exhibited several variation trends. The frequent occurrence of the nearly rotate corolla, the brighter yellow color, the reflexed upper corolla limb, the twisted corolla tube and reduction in pubescence suggest former introgression from the relict, *D. aridus,* now restricted to a limited inland range in southern San Diego County and northern Baja California. Each population—Toll Camp, Cushenberry and Yucca Valley—is more extreme in this trend as the location becomes farther removed from the San Gabriel Mountain contact. The *Diplacus* at Joshua Tree National Monument, Little San Bernardino Mountains, the farthermost extension of this series, exhibits the greatest shift toward *D. aridus* features.

The desert populations also show a higher frequency of the automatic selfing mechanism described above. Among cismontane *Diplacus* this feature is rare; in the Toll Camp population, some of the flowers in at least 50% of the plants express it sometime during a given flowering period. As a possible result of this increased autogamy, a number of desert *D. calycinus* populations contain a high frequency of apparently nonadaptive structures, e.g., extremely elongated and structurally weak styles, some resting on the lower lip of the corolla, and an increase or decrease in the number and kinds of flower parts. These variations usually reduce the pollination and fertilization success in diverse ways.

SAN JACINTO MOUNTAIN

The *Diplacus* populations of the San Jacinto Range correspond morphologically and ecologically with those of the San Bernardino Mountains. Though *D. longiflorus* influence is apparent at low elevations above Banning and Hemet, and the Hemet Reservoir population contains introgressed features of *D. aridus,* all are basically *D. calycinus* growing in Rock Rrevice habitats (fig. 21).

The populations existing in the desert climates exhibit the same trend toward automatic selfing and the expression of deleterious characteristics as the San Bernardino Mountain populations. One example in the Banning population, elevation 3,000 feet, had the two lateral lobes of the lower corolla limb reduced to green leaf-like structures, the number of stigmatic lips increased to three, and the pollen totally aborted. Several degrees of this aberration were expressed by different plants.

SAN JOSE AND PUENTE HILLS

The avenue of *D. puniceus* introgression to the San Gabriel Range is through the San Jose Hills contact near Glendora. At this point, a distance of less than one mile separates these two land forms and their populations of *Diplacus.* Completing the gene-flow trail from the Pacific Coast to the San Gabriel Mountains are the Puente Hills and the Santa Ana Mountains. The Puente and San Jose Hills have a low, rolling profile and are located 10 to

30 miles inland; thus the Insolated Hillside habitat prevails. The variable light to heavy soils are derivatives of numerous kinds of elevated sedimentaries and alluvia. Because of extensive agricultural practices, particularly cattle ranging, *Diplacus* populations are limited to a few fenced-off areas of Coastal Sage Scrub and Southern Oak Woodland, and to the numerous disturbances along winding trails, roadways, and ravines that are unavailable to the cattle.

Diplacus populations were sampled at Glendora, Puddingstone Dam, and Kellogg Hill in the San Jose Hills; La Brea Canyon, Carbon Canyon, Turnbull Canyon, and Prado Dam in the Puente Hills. These populations exhibit a wide range of orange-flowered *Diplacus* variants skewed toward *D. puniceus*. Frequently scattered in the populations are individuals expressing one or a combination of features: small flowers; red color hues; calyces not inflated; stem tips, pedicels and calyces glabrous; floral tubes shortened and angled moderately.

SANTA ANA MOUNTAINS

The low-elevation Santa Ana populations that lie adjacent to the Puente Hills contain *Diplacus* having a similar appearance to those that occur in the Puente and San Jose Hills. However, the *Diplacus* at the middle elevations below 4,000 feet, e.g., the highly insolated cismontane slopes above Silverado Canyon, show little of the *D. puniceus* influence but instead have the features of the San Gabriel race of *D. longiflorus*. On the less insolated northeast side of the 4,000-foot divide, limited populations of *D. clevelandii* grow in the loose, woods soil and partial shade of second-growth Southern Oak Woodland. Farther south the divide rises to its highest elevation, 5,680 feet, at Santiago Peak. Occurring on this exposed, wind-swept summit is *D. calycinus* in its typical Rock Crevice habitat.

On the inland side of the Santa Ana Mountains, from Indian Canyon to the summit of Santiago Peak, four *Diplacus* species occur in four different habitats: along the base, *D. puniceus* in a Temperate Hillside habitat; at the middle elevations, *D. longiflorus* in an Insolated Hillside habitat; within proximity of the summit, *D. calycinus* in a Rock Crevice habitat; and in scattered populations on the east side of the divide, *D. clevelandii* in the loose organic soils and partial shade of woodland and open chaparral. In the middle of their respective habitats these species retain their identity, yet occurring along the margins between them are numerous gradient examples of hybridization and backcrossing. The nearest other population of *D. calycinus* is over 30 air miles away. Though surrounded by three contaminating species, the Santa Ana *D. calycinus* is equivalent to the higher montane populations of the Transverse ranges.

The Temescal population at San Juan Pass (see above) consists of the Santa Ana Mountains *D. puniceus* as it occurs along the inland northeast base and low divide nearer the coast.

The Santiago Canyon population (fig. 10), occurring in an Insolated Hillside habitat on a southwest, cismontane slope of the Santa Ana Mountains, is typical of *D. longiflorus* existing in close proximity to *D. puniceus*. The primary differences between the San Diego race, as I shall call this form, and the San Gabriel race are the shorter floral tube, the shorter and less expanded calyx, the absence of pubescence, and different parentage of the former. The ecological difference between Temescal and Santiago is the exposure of the habitat which results in the greater amount of insolation at Santiago. Though the coastal slope of the Santa Ana Mountains receives one-third higher annual rainfall than the inland side, and though Temescal Wash and the hills to the northeast have a semi-desert climate and vegetation, the coastal southwest side also experiences two-thirds more evaporation from the larger amount of insolation it receives (Olmstead, personal communication). Also, the degree of insolation on the inland side is decreased by the greater relative steepness, thus keeping many slopes in constant shadow or at least protected from long periods and large amounts of direct solar radiation.

SAN JOAQUIN HILLS (Laguna Population)

During the months of April and May the San Joaquin Hills are dominated by the red-orange color combinations of flowering *Diplacus.* Along the Laguna Canyon road these color forms are numerous, and the range of variation appears wide. However, many of the flowers are bright red when newly opened but fade to various hues and intensities of orange and faded red during the days of high insolation. Consequently, the total variability of flower color is not entirely due to inherent color difference but also to the inherited degree of fading response to higher amounts of insolation. Each year, due to human-caused disturbance to the Coastal Sage Scrub community, e.g., roads, farming, cattle ranching, hunting clubs, and home building, many of the possible *Diplacus* recombinants successfully complete their life cycle and release copious amounts of seed, assuring future variability for all open habitats. Few areas are undisturbed, even the most stable vegetation is riddled with animal trails, burrows, and nests. In spite of this, plants of *Diplacus* in the less disturbed areas are surprisingly uniform.

From previous trends in the Santa Ana Range, a more extreme form of *D. puniceus* would be expected near the coast. If the Laguna Canyon population is compared with Santiago Canyon of the Santa Ana Mountains, this expectation is found to be true. By contrasting Laguna with Temescal of the Santa Anas, however, the opposite correlation is seen, i.e., Temescal is more extreme (fig. 8–10, 12, 20–21). Note, however, the Laguna population occurs five miles inland; the extreme coast is completely occupied by private homes and business, and most of the *Diplacus* has long ago disappeared.

PALOMAR MOUNTAIN

Though not strictly within the Laguna Series, Palomar Peak, elevation 6,125 feet, in the Agua Tibia Mountains of San Diego County, provided an observational checkpoint from which to compare the sequence of populations and habitats observed on the inland side of Santiago Peak in the Santa Ana Mountains. Except for the absence of *D. clevelandii,* the south side of Palomar Mountain exhibited a sequence of *Diplacus* species and habitats quite similar to the Santa Ana series. *Diplacus calycinus* inhabits the Rock Crevice habitat at the higher elevations, *D. puniceus* grows in the Temperate Hillside habitat at the base, and *D. longiflorus* occupies the Insolated Hillside habitat between the two. (If *Diplacus* is observed only from the mountain roads, the variation along the disturbed margins presents a confusing picture). When the lower habitats are overlapped, disturbed or otherwise open, swarms of hybrids abound. The more stable and closed vegetations contain the more uniform populations of *Diplacus.*

PERRIS PENEPLAIN

Occupying 400 square miles of rolling hills and elevated alluvial plains between the San Jacinto and Santa Ana Mountains and north of Palomar Mountain, is the Perris Peneplain. The possible occurrence of *Diplacus* introgression between the three ranges called for a general sampling of the area.

I found that, in many places, the widespread activity of agriculture confined *Diplacus* to the usual disturbed habitats. *Diplacus longiflorus* was found vacillating widely between marginal *D. calycinus,* west of Riverside, and *D. puniceus* in lower Quail Valley. In 1958, the sloping jumble of granite boulders on the west face of the earth-fill dam at Lake Mathews was dotted with a brilliant array of these variants. Before the invasion of man and subsequent land clearing and draining of San Jacinto Valley Lake, *Diplacus* introgression between the three mountain systems may have been extensive, viz., the *D. longiflorus* influence apparent in the lower elevation populations in the San Jacinto Mountains above Banning and Hemet. But at present, only a limited amount of genetic influence is flowing between mountain ranges through the Perris Peneplain.

RESULTS OF POPULATION ANALYSIS: SAN DIEGO SERIES

Because of the taxonomic and ecological discontinuities present in the populations of the coast-to-desert Laguna Series, and because of the south coast influence indicated in the Temescal, Laguna and Palomar populations, I decided to test these findings by analyzing a similar though limited series of populations in San Diego County.

As an example of *Diplacus puniceus,* the La Mesa population in Mission Valley was sampled first. I selected Point Loma next because of an apparent close relationship between *D. puniceus* and the insular *D. parviflorus.* I reasoned that, if such were the case, the more extreme *D. puniceus* would occur on the more temperate coastal headlands. The Lakeside population proved to be an ideal location for checking the ecological isolation between *D. puniceus* and the San Diego race of *D. longiflorus* where there habitats are adjacent.

LA MESA

This population occurred ten miles from the coast growing with sparse Coastal Sage Scrub on the rolling hills and mesas of heavy red adobe soil. I use the past tense advisedly because the population that I measured has since been exterminated by the rapid expansion of human "progress."

The *Diplacus* measurements of La Mesa correspond very nearly to those of Temescal in the Santa Ana Mountains (fig. 21–22). The *D. puniceus* of La Mesa were slightly more extreme in color and throat orifice, and decidedly more abundant.

POINT LOMA

With the Pacific Ocean on three sides, the Point Loma habitat has the most temperate climate of any *Diplacus* population yet measured. Except for the Channel Islands, the continuous offshore breezes provide one of the narrowest temperature ranges in California.

As in La Mesa, the soil is a heavy clay derived from terraced marine sedimentaries. The vegetation growing there is predominantly Coastal Sage Scrub.

When compared with the population at La Mesa, the *D. puniceus* at Point Loma had more uniformly bright red corollas (Munsell 7.5R3/6), and decidedly longer pedicels (fig. 21–22). Because these morphological variances could have been phenotypic expressions of the climatic differences between the two locations, seed lots were gathered from both and grown together in the garden. From them, I selected 50 plants per population which expressed the total range of variation. The same morphological variances measured in the natural populations were expressed in cultivation.

LAKESIDE

North of Lakeside the road to Ramona crosses the San Diego River wash and commences climbing up the foothills of the Cuyamaca Mountains. The elevation at this point is only 500 feet; the distance from the coast is 20 miles; the soils are heavy.

Scattered in the open Chaparral, *Diplacus puniceus,* La Mesa-like, grows on the low western foothill slopes. On the east slope of a low ridge a few hundred feet from *D. puniceus,* I found a population of large flowered, pastel-orange *Diplacus* growing exclusively among the boulder outcrops in the partial shade of coastal live-oaks. In collecting the sample from the latter population, every effort was made to select the plants which were most like *D. puniceus.* Even so, I was not able to demonstrate a gradient or cline between the two populations. In spite of indications that some introgression does occur, e.g., low dilutions of red flower color (fig. 21), preferential selection by the different habitats keeps the two entities morphologically and ecologically distinct.

This large-flowered *Diplacus* is distributed throughout the Peninsular Range in San Diego County. Morphologically it is similar to the San Gabriel race of *D. longiflorus* except that the plant is glabrous, the calyx shape is *D. puniceus*-like, the lower corolla

limb is not extended, and the upper limb is not reflexed. The Santiago Canyon population in the Santa Ana Mountains is transitional between the two. From its distribution it appears more resistant to cold than *D. puniceus,* and perhaps it requires a lighter soil and more soil moisture. For the time being I shall regard this entity as a San Diego race of *D. longiflorus.*

INTERIOR POPULATION

I made several collecting trips through the mountains and desert interior of San Diego County, that ranged from Lake Henshaw, Santa Ysabel and Ramona, to Descanso, Potrero, El Campo, and Jacumba, an area of some 1,200 square miles. On the lower coast-facing slopes, *Diplacus puniceus* influence is very evident. At the higher elevations the red color drops out, the pedicel is shorter, the flower size is larger, the stigma and anthers are included, and the populations become more uniform, but the calyx shape and glabrous condition of *D. puniceus* remain. These populations I am considering as a San Diego race of *D. longiflorus* (fig. 5–6). This group has a long nomenclatural history of synonyms that involve various combinations of "longiflorus", "linearis", "australis", "glutinosus", and "aurantiacus" within either *Mimulus* or *Diplacus.*

TABLE 4. *Diplacus populations*[a]

LOCATION AND POPULATION NAME	ELEVATION	DISTANCE INLAND	HABITAT	DIPLACUS SPECIES
		LAGUNA SERIES		
San Joaquin Hills				
Laguna Canyon	100 ft.	5 mi.	Temperate Hillside	*D. puniceus*
Santa Ana Mts.				
Santiago Canyon	1250 ft.	15 mi.	Insolated Hillside	*D. longiflorus*
Temescal Canyon	1500 ft.	24 mi.	Temperate Hillside	*D. puniceus*
San Gabriel Mts.				
Little Dalton Canyon	2700 ft.	35 mi.	Insolated Hillside	*D. longiflorus*
Thompson Creek Wash	1750 ft.	35 mi.	Insolated Hillside	*D. longiflorus*
Potato Mtn.	2500 ft.	36 mi.	Insolated Hillside	*D. longiflorus*
Sierra Sub-station	3200 ft.	38 mi.	Rock Crevice	*D. calycinus*
San Antonio Falls	7000 ft.	45 mi.	Rock Crevice	*D. calycinus*
San Bernardino Mts.				
Waterman Canyon	3000 ft.	52 mi.	Rock Crevice	*D. calycinus*
Toll Camp	4500 ft.	60 mi.	Rock Crevice	*D. calycinus*
San Jacinto Mts.				
Banning	3000 ft.	55 mi.	Rock Crevice	*D. calycinus*
Idyllwild	6000 ft.	55 mi.	Rock Crevice	*D. calycinus*
		SAN DIEGO SERIES		
Point Loma				
Point loma	100 ft.	0 mi.	Temperate Hillside	*D. puniceus*
La Mesa Hills				
La Mesa	375 ft.	10 mi.	Temperate Hillside	*D. puniceus*
Cuyamaca Mts.				
Lakeside	500 ft.	20 mi.	Rock Crevice	*D. longiflorus*

a. Only populations in which 25 or more individuals were analyzed are included in this table.

The desert locations include *D. aridus* near the Mexican Border and, according to McMinn (1951), mixtures of *D. ardius* and *D. calycinus* at Borrego Springs.

Formerly, *D. clevelandii* was collected near Descanso and Cuyamaca Peak. In recent years, however, attempts to re-discover it have failed.

At this time, it is impossible for me to evaluate, with any finality, the inherent relationships and speciation in the *Diplacus* taxa of interior San Diego County. Their distributions are incompletely known, and the habitat specifications are indecisive. A more comprehensive population study is indicated for the future.

DISCUSSION

VARIATION AND ITS IMPLIED SIGNIFICANCE

If one examines populations of *Diplacus* growing in stable plant communities, many of them prove to be relatively uniform within themselves. But if groupings of populations from different regions are compared, conspicuous differences become apparent. Justifiably, students of *Diplacus* have recognized these regional groups as taxonomic entities. Difficulties arise, however, when existing taxonomic treatments are applied to certain unusually variable populations. In such cases one population may include individuals that key, respectively, to two or more formal taxonomic units.

A case in point is the outcrop population at Thompson Creek Wash, San Gabriel Mountains. The data from this population indicate that the identified "species" are, in fact, recombinant products of introgressive hybridization which commonly appear only in ecologically open habitats where the intensity of biotic competition has been reduced. These variable arrays of progeny are formed when *D. puniceus* from the coast and *D. calycinus* from the higher mountains introgress and their genes recombine with those of *D. longiflorus* in the insolated foothills.

An obvious and disconcerting feature in these segregating populations is the red-flowered *Diplacus* that appears discontinuously throughout many of the hills and foothills of Los Angeles, southeastern Ventura, western Riverside, and Orange counties. This entity has been called *Diplacus rultilus* but has been treated more commonly as a variety of *D. longiflorus*. Adele Grant (1924) collected it at Santa Susanna Pass, Ventura County, and described it as a variety of *Mimulus longiflorus*. At the same time, she cited other specimens from as far east as San Antonio Canyon above Claremont. McMinn (1951) made it a "binom", *Diplacus rutilus*, and extended its distribution to western Riverside County. If the specimens exhibited a more glabrous and less campanulate calyx, both authors considered them as *D. puniceus* hybrids. In the San Jose Hills, both *D. rutilus* and hybrids involving *D. puniceus* were considered to be present.

At the beginning of this study, the flower color of *D. rutilus* from Santa Susanna Pass was measured as Munsell hue 2.5R3/7 and given a hybrid index value of six. Though large numbers of red-flowered *Diplacus* plants were measured, including *D. parviflorus* seedlings from Santa Cruz Island, not one, other than the Santa Susanna Pass specimens, reached this intensity of dark, velvety red. Instead, all of the red individuals from Los Angeles, Orange, and Riverside counties fell within the color range of *D. longiflorus*, 5YR7/11 and *D. puniceus*, 7.5R3/6, i.e., between salmon-orange and bright scarlet red (fig. 21).

In my estimation, the red *Diplacus* occurring in west Los Angeles, Riverside, and Orange counties are recombinants introgressed with *D. puniceus*. The *Diplacus* with the dark red flower color and velvety corolla texture from the region of Santa Susanna Pass is unique and probably arose locally as a recombinant or mutant. I consider it to be only a color form of *D. longiflorus*.

According to V. Grant (1957), hybridization is one of the four fundamental factors contributing to the obscurity of species lines in plants. *Aquilegia, Ceanothus, Clarkia, Delphinium, Gilia, Iris, Pinus,* and *Quercus* are but a few of the western genera, besides *Diplacus,* where hybridization has blurred the boundaries between species. As has been pointed out by Tucker (1952a) for the *Quercus dumosa* complex, Alva and V. Grant (1956, 1960) and V. Grant (1957) for the *Gilia tenuiflora* group, by Lenz (1958, 1959) for the Californicae series in *Iris,* and by others, to regard all intergrading entities in such groups as subspecies would obscure obvious morphological differences and confuse rather than clarify their systematics. The use of Lotsy's term, syngameon, for a group of hybridizing species was proposed by V. Grant (1957). The entities in a syngameon may vary

from discrete species to semispecies and even remnants of species. These gradations of speciation can result from either the establishment of an intermediate population bridging two species, or the submergence of one converging species into another, or the formation of a single secondary species from two merging species (compare V. Grant, 1957). In the course of its evolution, *Diplacus* has probably traversed all of the above courses.

Consideration should be given to two hypotheses regarding the phylogeny of the group comprising *D. calycinus, D. longiflorus,* and *D. puniceus.* The first, proposed by McMinn (1951), holds that *D. longiflorus* is a polymorphic, ancestral species from which *D. calycinus, D. puniceus,* and others were derived through adaptive radiation. An alternative hypothesis that I wish to suggest is that *D. longiflorus* and *D. puniceus* are both derived and that *D. calycinus* and *D. parviflorus* are ancestral. This hypothesis is based on paleontological and ecological criteria in addition to morphological evidence.

Both *D. puniceus* and *D. longiflorus* exist in habitats that apparently have been derived recently when compared to those of *D. calycinus.* According to Axelrod (1957, 1959), the topographical and climatic changes that were occurring during the latter half of the Tertiary gave rise to a Mediterranean climate and thus the Mediterranean Scrub vegetation at the latter part of the Pliocene. The plant communities inhabited by *D. calycinus* probably existed before the development of the Coastal Sage Scrub and Chaparral habitats of *D. puniceus* and *D. longiflorus. Diplacus longiflorus* is intermediate: morphologically, climatically, and geographically it lies between the extremes of the species that border it, and its range of variability is directly affected by these adjacent groups. Thus, the subspecies differences between the San Gabriel and San Diego races may be due to the past and present species bordering these areas and the preferential selection of *Diplacus* variability by the diverging environments.

I believe that *D. calycinus* is the inland ancestral contributor to the evolution of both *D. longiflorus* and *D. puniceus,* but its own distinctness remains relatively unblemished and uniform due to the exclusion of foreign germ plasm by the more extreme climatic conditions of its habitat. The *D. calycinus* populations on Santiago Peak in the Santa Ana Mountains and on Palomar Mountain in the Agua Tibias are cases in point. Surrounded and isolated, these populations have retained their integrity. However, where *D. calycinus* remains in the desert woodlands, it shows distinctly the influence of *D. aridus.*

There are locations where two uniform populations, each containing different kinds of *Diplacus,* are located within the same limited territory and still reproduce themselves true to type. Invariably in such cases, the two populations occur in different ecological niches. An example of this is in San Antonio Canyon, where *D. longiflorus* inhabits the open chaparral of a sun-beaten slope while *D. calycinus* clings to the vertical north face of an old river bank a few feet away. Since *D. calycinus* can not compete with the chaparral, and *D. longiflorus* is unable to support its heavy branching system on vertical cliffs, these two demes are ecologically isolated.

Prior to this study, the role of ecological isolation had not been invesitgated in *Diplacus,* yet there is little doubt of its importance in the maintenance of co-existing populations in this genus as well as other western North American genera. For example, Anderson (1954b) showed the ecological isolation of certain *Adenostoma fasciculatum* biotype groups in a wide variety of open and closed niches. The integrity of the interfertile *Salvia apiana* and *S. mellifera,* as demonstrated by Epling (1947) and later by Anderson and Anderson (1954), results, at least in part, from their preferential selection by different habitats. Lenz (1958, 1959) discovered ecological differences to be a basic cause of species separation in the California series of *Iris.* Muller (1952), Tucker (1952a, b; Tucker and Muller, 1958; Tucker and Haskell, 1960) and other students of *Quercus* found ecological control of hybridization to be the principal force maintaining species distinctions in the

western oaks. Lewis and Epling (1959) believe that *Delphinium gypsophilum* arose rapidly as a diploid product of hybridization and subsequent ecological isolation in a habitat that was geographically and ecologically intermediate between those of the two putative parent species. The two closely related species of pines, *Pinus ponderosa* and *P. jeffreyi,* as Haller (1959) suggested, and Wagener (1960) confirmed, are ecologically separated by low winter temperatures operating at the seedling stage.

According to Nobs (1951; pers. comm., 1960), certain coastal and inland species of *Ceanothus* are isolated ecologically except where the habitats overlap or in some other way are separated imperfectly. In these locations are found the confusing gradations of morphological variability, a situation similar to that of *Diplacus* and numerous other California genera.

Hybridized habitats (Anderson, 1949) are abundantly produced in California both naturally and artificially. The hybridizing *Diplacus* respond to many of these open and varied niches with a profuse display of recombination. As plant and habitat succession gradually close the open door, the numbers and kinds of recombinations become narrowed and regulated according to the preferential selection by the habitat until ecological isolation once again exists between certain different recombination types (Anderson, 1954b; Anderson and Anderson, 1954; V. Grant, 1958).

Until recent years, introgressive hybridization was not regarded as a progressive evolutionary force that could lead to the formation of new species. Instead, its principal attribute was considered to be the convergence of previously distinct species, though race and subspecies development were believed possible (compare Stebbins, 1950).

Recently, however, an increasing number of evolutionists have been establishing rapid environmental change and hybridization as important stimuli to major evolutionary advancement (Simpson, 1949, 1953; V. Grant, 1953, 1957, 1958; Anderson and Stebbins, 1954; Stebbins, 1959). According to Simpson (1949, 1953), past bursts of rapid evolution are probably preceded by accelerated rates of change in the physical environment that open new habitats for pre-adapted organisms. Verne Grant (1953) proposed that the homogamic complex, in which hybrid products are diploid and fertile, possesses an open, and thus a progressive, system of evolution. Anderson and Stebbins (1954) and Stebbins (1959) concurred that hybridization between differentially adapted populations would provide a ready and variably rich source of new adapitve recombinations for these open ecological niches of a rapidly changing environment.

SUMMARY

1. *Diplacus* is a genus of semi-shrubs found from southern Oregon to northern Baja California. The group has its center of diversity in the summer-dry vegetation of California and is scattered inland discontinuously to the Sierra Nevada and southern California deserts.

2. A state of flux in *Diplacus* systematics has resulted from the variability in and between *Diplacus* populations. The present investigation attempts to describe and interpret this variation and reveal its causes within the limits of southern California. Tentatively, five *Diplacus* species are recognized in southern California: *D. calycinus, D. longiflorus, D. puniceus, D. aridus,* and *D. clevelandii.* Because of conspicuous hybridization obscuring the discontinuities between the species, *D. calycinus, D. longiflorus,* and *D. puniceus* are considered to be more critical taxonomically. The geographical limits of these taxa are defined more definitively than before.

3. The *Diplacus* populations of southern California are arranged into two series: the Laguna Series, from the Pacific coast to the western margin of the Mojave Desert; and the San Diego Series, from Point Loma to the Cuyamaca Mountains. The Laguna Series comprises the greater area and larger number of populations.

4. For each principal population sampled, at least 25 individuals were analyzed. Smaller collections were measured between and adjacent to the principal populations. All specimens were measured while fresh, using selected morphological features. The methods by which these data are presented are described above.

5. Generalized habitats for the three principal *Diplacus* species are determined to be the Temperate Hillside habitat for *D. puniceus,* the Insolated Hillside habitat for *D. longiflorus,* and the Rock Crevice habitat for *D. calycinus.* Mentioned later are the Rock Crevice habitat of *D. aridus* and the Woods-type soil of *D. clevedandii.*

6. *Diplacus* is principally an outcrossing group of interfertile diploid species. Of special note is the sensitive stigma, a mechanism for outcrossing that has become adapted in *D. calycinus* for automatic selfing. Though the hummingbird is the most prevalent pollinator, the hawk moth and long-tongued cyrtid fly, *Eulonchus,* are additional visitors. Few facts are known concerning the dispersal and germination of the numerous and tiny *Diplacus* seed.

7. Chromosome numbers and pollen fertility samples are given for a number of *Diplacus* species and their hybrids. Though some hybrids and backcrosses show some lowered fertility, most are both viable and vigorous. All species and the interspecific crosses that were examined are diploid, n=10, and meiosis in the PMC's appeared normal.

8. The results of the populaiton analysis show that *D. calycinus, D. puniceus,* and *D. longiflorus* are specific to certain environments. *Diplacus calycinus* exists in the rock crevices of Yellow Pine Forest and adjacent desert woodlands; *D. puniceus* occupies the temperate foothills and headlands of the Pacific coast, mostly in Coastal Sage Scrub, open Chaparral, and their ecotone; *D. longiflorus* occurs on the highly insolated, west-facing slopes of the inland foothills in an ecotone of open Chaparral and Coastal Sage Scrub. Differences are described between two races of *D. longiflorus:* the glabrous San Diego race and the pubescent San Gabriel race.

9. The breakdown of ecological isolation and the occurrence of introgressive hybridization are important causes of population variability. Interspecific hybridization along the zone of species contact is followed by introgression into the population. Ecologically open habitats allow extreme recombinants to succeed. The kinds and causes of open habitats and differential patterns in population variation are discussed.

10. When compared regionally, populations of uniform *Diplacus* exhibit conspicuous discontinuities that justifiably allow their recognition as taxonomic units. Due to disturbance or intergrading conditions and the appearance of introgressants in the open habitats, the above distinctness becomes blurred, resulting in taxonomic confusion. The red-flowered variants in the *D. longiflorus* populations of four counties is a case in point. In this study, *"D. rutilus"* is reserved for the Santa Susanna Pass populations in northeastern Ventura County. These populations, with their deep, velvety red flowers, are considered to constitute only a form of *D. longiflorus,* with which they agree in other respects. The other red-flowered *Diplacus* are treated as introgressive products from the coastal *D. puniceus.*

11. In the past, *D. longiflorus* has been proposed as the putative ancestor that gave rise to *D. calycinus* and other *Diplacus* species by adaptive radiation. Additional ecological and paleontological evidence now suggests that *D. calycinus* exists in a geologically and vegetationally older habitat than *D. longiflorus.* With the insular species, *D. parviflorus, D. calycinus* may be ancestral to both *D. puniceus* and *D. longiflorus.*

12. The five interbreeding diploid species of Southern California *Diplacus* constitute a species group called a syngameon. The qualifications of the syngameon for rapid progressive evolution in a changing environment are examined.

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